VOLUME 131 PART I JULY 1958

QL
1
.Z8

PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY

OF

LONDON

UNIVERSITY
OF MICHIGAN
OCT 3 1958
MUSEUMS
LIBRARY

LONDON
PUBLISHED BY THE SOCIETY
SOLD AT ITS HOUSE IN REGENT'S PARK, LONDON, N.W.1

Price Thirty Shillings

THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON
THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

Editor . . . . . L. HARRISON MATTHEWS, F.R.S.
Clerk of Publications . . . G. B. STRATTON, M.B.E.

The **Proceedings,** founded in 1830, are published in royal octavo form and constitute the principal organ of the Society for the publication of original works in zoology, and for notices of the business transacted at the Scientific Meetings of the Society.

Two volumes are published annually; each volume containing four numbers. Price per volume £6; separate numbers £1 10*s.* 0*d.* each.

The **Transactions,** founded in 1833, are published in quarto form and contain those papers and monographs which by reason of the size of the illustrations, are better adapted for publication in that format. The " Transactions " are published at irregular intervals at prices varying in accordance with the cost of production.

OTHER PUBLICATIONS OF THE SOCIETY.

The Zoological Record, founded in 1864, is issued annually with the object of providing a complete list of references to publications in zoology in all its branches for each year of issue, the price of the complete volume is £8. The Society is unable to supply *complete sets* of the " Record " as several volumes are now out of print. The following volumes are available :—

Vols. 65–71 (1928–1934), 85 (1948) at £5 each.
Vols. 86–91 (1949–1954) at £6 each.
Vol. 92 (1955) at £8.

PHOTOLITHOGRAPH REPRINT. Vols. 1–20 (1864–1883). Obtainable only from Messrs. Butterworths, 88 Kingsway, London, W.C.2.

Complete set of 20 volumes, bound in cloth, price £160.
Complete set of 20 volumes, in paper covers, price £155.
Separate volumes, in paper covers, at £8 each.

Nomenclator Zoologicus. The five volumes contain the names of all the genera and subgenera in zoology from the 10th Edition of Linnæus 1758 to the end of 1945, with a bibliographical reference to the original description of each. Price 17½ guineas, postage extra. Price of the separate volumes : Vols 1–4 (1758–1935) ; Vol. 5 (1936–1945) 3½ guineas each, postage extra.

Advice on Pets. Price 1*s.*, postage extra.

Centenary History of the Zoological Society of London, by P. Chalmers Mitchell. 1929. Price 10*s.*, postage extra.

Index to Sir George Hampson " A revision of the subfamily Pyraustinae and family Pyralidae " published in the ' Proceedings ' 1898 and 1899. Price 10*s.* 6*d.* post free.

Some Suggestions on the Transport of Animals. Price 1*s.* 6*d.*, post free.

" Zoo "—The official guide to the London Zoological Gardens. Price 2*s.* 6*d.*, postage extra.

All communications concerning the Society's publications should be sent addressed to :

THE SCIENTIFIC DIRECTOR,
ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W.1,
ENGLAND.

1865
75
4V
Nest

THE NEST-BUILDING BEHAVIOUR OF DOMESTICATED CANARIES

BY

R. A. HINDE

Cambridge University Department of Zoology, Field Station for the Study of Animal Behaviour, Madingley, Cambridge

[Communicated by Dr L. HARRISON MATTHEWS, F.R.S.—accepted 12th November 1957]

(With 10 figures in the text)

CONTENTS

		Page
1.	Introduction	2
	(a) General	2
	(b) Material and methods	2
2.	Description	3
3.	Nest-site selection	4
4.	Time sequence of nesting activities	5
	(a) The normal nest-building cycle	6
	(b) Relation of nest-building activity to laying of first egg	6
	(c) Relation between nest-building and sexual behaviour	9
	(d) Cycles of nest-building activity	10
	(e) Nest-building by the male	10
5.	Motivational relationships between gathering, carrying and sitting (building)	12
	(a) Correlation between total times spent gathering, carrying and sitting	12
	(b) Behavioural measures of building activity	14
	(c) Relation between building activity and total time in each constituent activity	17
	(d) Relation between building activity and bout lengths of the constituent activities	20
	(e) Relation between the successive bout lengths in a building sequence	23
	(f) The appetitive/consummatory behaviour dichotomy	25
6.	Variations in the frequency of nest-building movements	28
	(a) General	28
	(b) Variations in frequency of scrabbling	29
7.	Control of the cessation of nest-building	30
	(a) General	30
	(b) Internal factors	30
	(c) External factors	31
	(d) Conclusions	33
8.	Effect of the nest pan on sitting bout length	33
9.	The selection of nest material	34
	(a) General	34
	(b) Internal factors	34
	(c) External factors	35
	(d) Conclusion	39
10.	Bizarre building habits	39
11.	Building behaviour of naive birds	44
12.	Conclusions	45
13.	Summary	46
14.	Acknowledgments	47
15.	References	47

1. INTRODUCTION

(a) *General*

The construction of a nest involves the functional integration of a number of different activities. Since birds of many species, brought up away from adults and in similar environments, construct the type of nest characteristic of their own species, the activities involved and the way in which they are integrated must depend in part on hereditary factors. Nevertheless the realisation of these hereditary factors involves environmental influences, and learning plays an essential part in nest construction. In these respects nest-building resembles, of course, other species-characteristic activities, but it is one which is particularly susceptible to study. In the work described here the nest-building of domesticated canaries was analysed in an attempt to elucidate some of the factors controlling the appearance, cessation and integration of the various activities involved. The building of a nest is, however, a complex process, and its understanding involves studies of many aspects of behaviour and physiology. It must therefore be emphasised that the generalisations contained in this paper represent only a first stage of analysis.

The conclusions reached here depend on observations of domesticated canaries, in an artificial and purposefully simplified environment. This was necessary, because most wild species desert their nests if subjected to only a small part of the interference which these canaries tolerated. It also has many advantages, for more than one pair could be watched at a time, and the conditions of building could be controlled. In point of fact, the building behaviour of domesticated canaries differs little from that of the wild species, and, under the conditions provided, the domesticated birds build quite adequate nests.* Further, the movements used are at least similar to those employed by many other passerine species (e.g. van Dobben, 1949 ; Kramer, 1950 ; Deckert, 1955 ; Marler, 1957).

(b) *Material and methods*

(i) Stock. Most of the birds used were of the Border variety, though in a few cases Rollers were also studied.

(ii) Cages. The cages were made of metal, of dimensions 110 cms. by 35 cms. by 30 cms., and with a wire netting floor. They have been described in detail elsewhere (Dunnett & Hinde, 1958). Each such cage contained one pair of birds.

(iii) Nest-pans. A standard plastic canary nest-pan, with a cup 10·5 cms. diameter and 4·5 cms. deep was hung on the wall of each cage : this was nearly always used by the birds.

(iv) Nest-material. Only two types of nest-material were provided—dried fine grasses in lengths of c.10 cms., and the body feathers of domestic pigeons. These were scattered over the floor of the cage in approximately equal quantities (i.e. so that each covered an equal area of the floor).

* Though Promptov (1956) claims that experience is necessary for building amongst branches (Original reference and translation kindly supplied by Dr R. J. Andrew).

(v) Pre-experimental treatment. Most of the birds were obtained from dealers a few months before each breeding season. Some of them were kept without nest-material during the intervening period.

Other birds were bred at the Station, and some of these were removed from the nest about eight days after hatching and placed in an adjacent wire-netting cage where their parents could feed them, but where they had no access to nest or nest-material ; they were also not permitted to watch other birds building. These birds were subsequently kept without material until their first spring.

(vi) Experimental procedures. Some of the birds were allowed material continuously. Others were given it only for the duration of the half-hour daily watch, after which it was removed from the nest-pan and floor of the cage. By this technique it was possible not only to witness all the effective building behaviour performed by an individual, but also to produce building rates much higher than those shown under normal conditions.

Other procedures are described in the text.

(vii) Recording. The normal procedure was for each pair to be watched for half an hour a day. The female's activity was recorded in one of two ways. Early in the study, her behaviour was recorded on graph paper which had a time scale previously marked on it ($\frac{1}{2}$ in.$=$10 secs.). By the use of suitable symbols it was possible to make a continuous record accurate to within about two secs. Later a Gregory-Russell recorder became available. This has a coding unit with keys, depression of each key causing the printing of the time and a letter or pair of letters on a strip of paper which moves on after each excitation (Gregory, in press). This enabled even more accurate records to be kept.

2. DESCRIPTION

Nest-building behaviour can be conveniently subdivided as follows :

(a) Inspecting. The bird perches on the nest-site or nest-pan, examining it closely.

(b) Gathering. In this study the nest-material was invariably scattered over the floor of the cage. When gathering, the bird hops over the floor, pecking from time to time at the material. At low intensity, pecks are rare and most of the time the bird merely examines the material closely. Even when it pecks frequently at the material, it does not necessarily pick it up ; and even when it picks it up, it may drop it without carrying it off. Indeed only when building activity is at its peak is the material picked up and carried off without any hesitation : more usually each piece of material is picked up and dropped many times, or mandibulated for long periods on the ground. Since the same feather may be toyed with in this way for a minute or longer, and then eventually carried to the nest, the delay seems to be a function of the motivation and not of the suitability of the material (van Iersel, 1953 has made a similar observation with regard to the Three-spined Stickleback, *Gasterosteus aculeatus*).

Gathering may include the pulling of strands of material away from a bunch, and various types of manipulation. Some females frequently took the material to the water trough and mandibulated it there—this may help to make the material more pliable (cf. Armstrong, 1955).

(c) Carrying. Carrying was considered to start when the bird flew up from the floor with material, and to end when the bird returned to the floor, placed the material, or sat in the nest, or dropped it. Just as gathering may involve much toying with material, so even when the female has flown off with it she may not carry it directly to the nest. Sometimes bunches of material would be carried to and fro for minutes on end, and then dropped aimlessly from a perch. Such behaviour occurs early in the season in many wild birds (e.g. Eliot Howard, 1929), but may be more common in cage birds which do not have to look for their food. When building activity is frequent, the material is carried straight to the nest. The change over from carrying to sitting (building), like that from gathering to carrying, thus depends only partly on external stimuli, the internal motivation also being important. It will be clear that both gathering and carrying consist of a number of different activities—but they form convenient categories for the present study.

(d) Placing. The material is placed in the cup while the bird either stands on the rim or sits inside and places the material under its breast.

(e) Sitting (building). The material is built into the nest while the female is sitting in the cup (or, in the early stages of nests built in branches, perching in the place where the cup will be). The movements used resemble those used by other passerines, and may be largely identical with them (e.g. van Dobben, 1949 ; Marler, 1957):

(i) Pulling and weaving. Loose pieces of material sticking up from the nest rim are seized in the bill, pulled towards the breast and pushed down into the cup. When performed without material, this behaviour consists in rather variable movements of the head.

(ii) Scrabbling. The female presses her breast down into the cup and pushes back hard with each leg alternately and in rapid succession.

(iii) Turning. While sitting in the nest, the female turns so that she is facing in another direction.

(iv) Pressing down. The bird sinks down in the cup, often expanding its body feathers. The body and wings are pressed into the cup and help to shape it.

(v) Wiping. While sitting in the nest the females passes her bill laterally along the rim of the nest. This movement was rare under the experimental conditions, probably because it is normally associated with the use of spiders' webs.

Sitting (building) can be distinguished from sitting (incubating) by the occurrence of these movements. In this paper " sitting " refers to the former.

3. NEST-SITE SELECTION

In the early stages of building, nest-material is carried about, only to be dropped at random—internal factors are apparently not yet sufficiently

strong for the thresholds of placing and sitting (building) to be reached. However at about this time, or even earlier, the female selects a site. The most obvious behaviour pattern involved is inspecting, which usually reaches a peak shortly before the main building activity (see p. 8). Often the female also sits in the site, and goes through some of the movements of building (e.g. turning, scrabbling) there, even though she has no material. In many other carduelines nest-site displays, in which the male sits in the site and calls the female to him, are common (Hinde, 1955), but amongst the canaries observed in this study it was the female who appeared to select the site. The males, however, often inspected the site, and this may have affected the females.

The nest-pans which were provided were almost invariably chosen—only occasionally during the second or later nestings did a female attempt to build elsewhere (e.g. in the corner of the cage).

Once the nest has been started, the nest itself is a potential source of nest-material. Occasionally females attempting to nest in the seed pan or corner of the cage would carry material *away* from the nest-pan, which suggests that the nest-pan itself does not provide stimuli necessary for placing unless it has previously been "selected". The fact that during normal building material is carried to the nest-site, rather than away from it, is thus apparently due to learning which occurs during the selection (see also Section 10).

It is uncommon for a female to build in two places simultaneously, especially when building is more than desultory. One female who was building vigorously carried material sometimes from the nest-pan to the corner of the cage, and sometimes vice versa, but this condition was temporary and the next day she was building normally in the pan. Once a female is building steadily in one place, it is often difficult to discourage her. When a female started to build in a cage corner, irregularly placed pieces of wood blocking off the corner were sometimes not effective in stopping her for several days. A similar limitation of responses to one out of a class of possible stimulus objects occurs also in the selection of territory, mate, and so on, and can be compared to the "imprinting" occurring in the mother-offspring relationship (Hinde, in press). Such learning was discussed by James (1892) under the "Law of inhibition of instincts by habits".

TABLE 1

Frequency of inspecting nest-site (a) during normal building; and (b) during watch immediately following (a) in which nest was removed from nest-pan.

Pair No.	No. days observations (30 mins. per day)	Total no. inspections in normal building (a)	Total no. inspections after nest removed (b)
26/55	3	8	30
23/55	6	9	26
19/56	9	4	21

Occasional inspection of the nest-site also occurs throughout building and subsequent phases of the reproductive cycle. It is particularly frequent

if the nest is disturbed in any way—for instance when the nest is removed from the nest-pan (Table 1). Amongst females who were allowed material for only one half-hour period each twenty-four hours, inspection was much commoner when material was not present than when it was (Table 2).

TABLE 2

Frequency of inspecting nest-site (a) with no material present ; and (b) after material added.

Pair No.	No. days observations (30 mins. per day)	Total no. inspections with no material (a)	Total no. inspections after material added (b)
2/56	9	81	2
9/56	4	54	1
26/56	9	27	0
27/56	3	36	18

4. TIME SEQUENCE OF NESTING ACTIVITIES

(a) *The normal nest-building cycle*

Figure 1 a–c illustrates the daily changes in nest-building behaviour shown by three females building in undisturbed conditions, as indicated by the observations in daily 30-minute watches. The details of the nest-building cycle vary greatly between individuals, but these examples are representative of common types. The following points may be noted here : they will be discussed in more detail later.

(a) The fluctuations in the total time spent gathering, carrying and sitting (building) run roughly parallel with each other, though sitting (building) does not appear until rather later than the others. The start of sitting (building) is rather abrupt (Section 5).

(b) The average bout lengths of gathering and carrying tend to be maximal just before (or after) intense carrying and sitting (building) respectively (Table 13.)

(c) The time spent feeding tends to be greater when building activity is low (Table 11).

(d) The proportion of building sequences which are completed, as shown by the ratios of the number of carrying to gathering bouts and of the number of carrying bouts which ended in placing to the total number, is greater when building activity is more intense, and/or towards the end of the nest-building cycle.

(b) *Relation of nest-building activity to laying of first egg*

Table 3 has been constructed to illustrate the occurrence of nest-building activity in relation to the laying of the first egg (Day 0). It shows the date on which the peak of inspecting (number of visits in 30-minute watch), gathering (total time, seconds, in 30-minute watch), placing (number per watch) and sitting (building) (total time, seconds, per watch) occurred at eight first nests and seven later nests. In some cases differences were apparent between

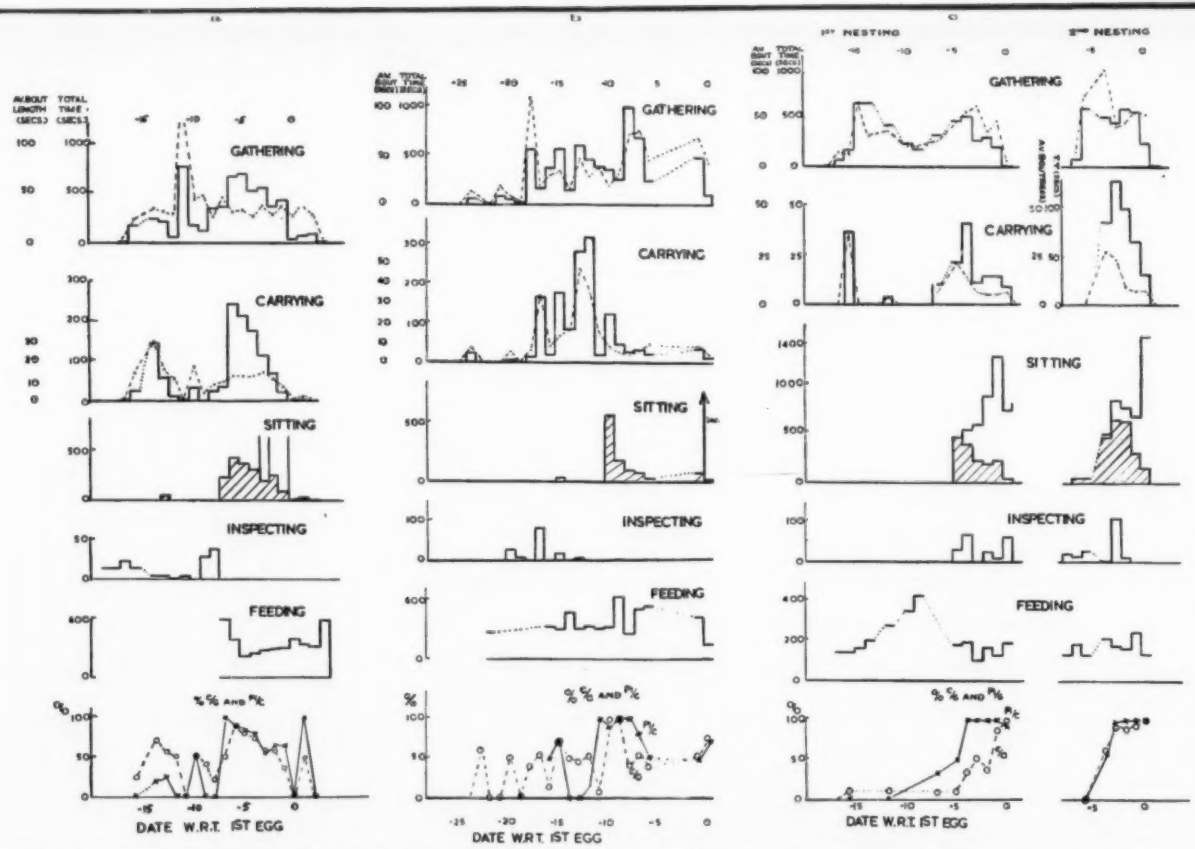


Fig. 1 a, b and c.—Daily changes in nest-building behaviour shown by three females. 1 c shows the first and second nestings of the same bird. In diagrams of gathering and carrying, histogram refers to total times per watch, and discontinuous line to mean bout lengths. In diagram of sitting, shaded portion refers to sitting (building) and unshaded part to sitting (incubating). In bottom diagrams continuous line indicates percentage of gathering bouts which led to carrying, and the discontinuous line to percentage of carrying bouts which led to placing.

TABLE 3

Occurence of various nesting activities, in relation to date of first egg, amongst birds with nest material continuously present.
Day 0 is date of first egg.

	Day												
	−12	−11	−10	−9	−8	−7	−6	−5	−4	−3	−2	−1	0
Peak inspecting 1st nests	1	2			1								
Ditto Later nests					1	1	1	1	2				
Peak gathering 1st nests					1		1	1	2	3			
Ditto Later nests								1	1	3	1		
Peak placings 1st nests						2	1	1	2	3			
Ditto Later nests							1	1	2		3		
Peak total time sits. 1st nests					1		1		2	2	1		
Ditto Later nests							2	1		2	1		
Material brought Peak day							1	1	8	5	3	2	2

(A few inconsistencies in the number of nests for which data are available in each column are due to breaks in the observations which prevented peaks being dated precisely).

first and later nests ; these are therefore shown separately on the table. It will be seen that :

(i) Most of the building activities occur rather earlier in relation to the laying of the first egg at first nests than at later ones, though there is little difference in the peaks of placing and sitting.

(ii) There is no significant difference between the peaks of gathering, placing and sitting (building), the means being days −3·3, −3·6 and −4·1 for later nests. Inspecting, however, occurs rather earlier than these (−5·6).

(iii) The last line of the table shows the occurrence of the peak weight of material brought to the nest—the mean here is −3·0. (This includes birds who built undisturbed and birds whose nests were removed daily : both had material continuously available. The two groups did not differ significantly).

Table 4 shows similar data for placing for pairs which were provided with material for the duration of the half hour daily watch only (see p. 3). The

peak placing (mean −2·2) is later than at nests where material was present continuously, the difference being significant ($P < 0{\cdot}05$). In addition, an arbitrary level of twenty placings per watch has been adopted to indicate the duration of moderate building activity.

TABLE 4

Occurrence of placing in relation to date of first egg amongst birds with material present for half an hour per day only. Day 0 is date of first egg.

	Day												
	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5
Number of placings 1st >20	2	3	1	3	1	2	1						
Number of placings, Peak	1			2	2	6	4	2					
Number of placings 1st <20						2	1		4	4	2		1

It is clear from these tables that individual variation in the relation between the peak of building and the laying of the first egg is very considerable, and this suggests that the causal relations between ovulation and associated processes on the one hand, and nest-building on the other, are not rigid.

(c) *Relation between nest-building and sexual behaviour*

Table 5 shows the mean number of occasions per watch on which the male mounted the female for copulation, and the mean number of occasions on which the pair touched beaks in courtship feeding, on the days before and after the laying of the first egg for all nests at which records were kept. The

TABLE 5

Occurrence of copulation and courtship feeding—all pairs.

	Day																
	−12	−11	−10	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4
No. of 30-min. watches	12	12	14	16	20	22	30	34	38	45	45	43	43	25	22	15	12
Mean no. of copulations per watch	·1	0	·1	·1	·1	·4	·3	·3	·4	·6	·6	·6	·4	·5	·4	·2	·2
Mean no. courtship feedings per watch	·8	·8	·6	·4	·5	·6	·9	1·0	1·3	·8	·9	1·0	·8	·8	·7	·9	·8

peak of courtship feeding is spread over the week preceding the day the first egg was laid. The peak of copulation is on days −3 to −1, slightly later than the peak of nest-building (see above).

(d) *Cycles of nest-building activity*

At the beginning of the season many females show successive cycles of nest-building activity, the peak of each cycle being followed by a reduction in activity even though no egg is laid. Some indication of such cycles is shown by two of the females whose behaviour is summarised in Fig. 1. Often each of the cycles is preceded by a peak in inspecting : sitting (building) is often absent from the earlier cycles. Further examples, taken from females whose nests were removed daily, are shown in Fig. 2, where the weight of material brought each day is plotted against the date. Similar cycles occur in the sexual and nest-building behaviour of other captive finches (*Fringilla* and carduelines) and tits (*Parus* spp., personal observation).

(e) *Nest-building by the male*

In most carduelines the nest is built by the female, though the male may bring material and help to an extent which varies both individually and between species. Amongst the canaries watched in this study the males often gathered and carried material, and occasionally placed it, but their direct contribution was negligible compared with that of the females.

The building activity of the male was recorded at eleven nestings. The mean frequency of inspection and placings are shown in Table 6. The peak of each of these activities in the male, though rather indefinite, occurs slightly earlier with respect to the laying of the first egg than in the female (cf. Table 3).

TABLE 6

Incidence of male inspections and placings in relation to laying of first egg. Based on eleven nestings.

	Day																
	−15	−14	−13	−12	−11	−10	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2
Mean no of inspections per watch	2·0	0·8	0·4	2·0	1·1	1·6	1·8	0·3	0·7	1·7	0·4	0·1	0·3	0·7	0·3	0·1	0·5	0
Mean no. of placings per watch	0	0	0·2	0·2	0	0·4	0·5	0·5	0·9	0·6	0·3	0·3	0·4	0·8	0·6	0·7	0·3	0

It seems likely that the daily changes in the male's behaviour are due to a direct effect of the female's behaviour rather than to internal (e.g. hormonal) changes which are more or less independent of immediate external stimuli. Although the male does little actual building, his behaviour may influence the female's between bouts of nest-building. Males were particularly likely to sing while their mates were feeding, and this may affect the female.

Fig.

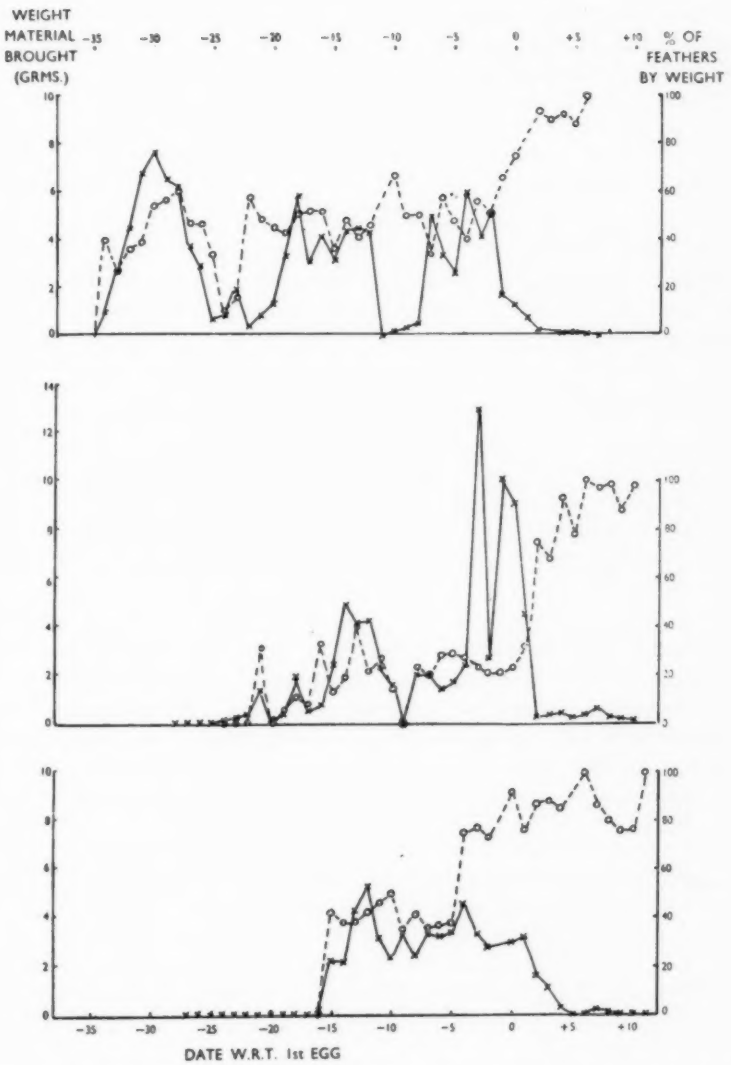


Fig. 2.—Fluctuations in building activity, during the weeks preceding the laying of the first egg, in three naive females which were provided with material continuously but whose nests were removed from the pan daily. Continuous line—weight of material removed from nest. Discontinuous line—percentage of feathers in material removed from nest.

TABLE 7

Relation of male building activity to incidence of copulation. Watches in which the female placed at least once only included.

No. of copulation attempts involving male landing on female's back in watch	0	1	2	>2
No. of watches	67	19	15	7
Mean no. of placings per watch by male	0·72	0·16	0	0

Table 7 shows that male building behaviour is less frequent in watches in which copulation occurs than in those in which it is absent. Superficial observation suggested that a similar relation holds for courtship feeding.

5. MOTIVATIONAL RELATIONSHIPS BETWEEN GATHERING, CARRYING AND SITTING (BUILDING)

Gathering, carrying and sitting (building) are functionally related activities (or, to be more precise, groups of activities); for the nest to be built they must be performed one after the other in the correct sequence. In this section some evidence on the causal relationships between these three activities will be considered.

(a) *Correlation between total times spent gathering, carrying and sitting*

We have already seen that the total time per watch spent in each of these activities reaches its peak at about the same time with respect to the laying of the first egg, and that they wax and wane roughly in parallel. Correlation coefficients between the total times of gathering, carrying and sitting for the period preceding the laying of the first egg are shown in Table 8 for six nests—

TABLE 8

Correlation coefficients between total times of gathering, carrying and sitting (building) per daily watch at six nests. X indicates nest removed daily.

Nest	N	Corrln. between gathering and carrying	Corrln. between carrying and sitting (building)	Corrln. between gathering + carrying and sitting (building)
33/56	10	+0·31	+0·79	+0·76
19/56x	10	+0·61	+0·51	+0·63
11/56	18	+0·72	+0·92	+0·81
34/56x	14	+0·30	+0·51	+0·41
2/56x	7	+0·28	+0·91	+0·37
4/57	14	+0·63	+0·58	+0·79

all days on which the female incubated being omitted from the calculations. At some of these nestings the material was removed daily, so that the external stimulus situation was more or less constant at the start of each day's watch. The coefficients are consistently positive, suggesting a relationship between the causal factors affecting the several activities.

Such a positive correlation could, of course, be due to the fact that gathering brings the female into a stimulus situation where carrying is likely to be evoked, and carrying brings it into a stimulus situation for sitting. That such changes in the external stimulus situation are not the only factors concerned is shown by :

(a) Sitting is sometimes not preceded by gathering and carrying. (Carrying, of course, cannot be identified as such unless preceded by gathering). This is particularly frequent in the period of site selection, when the female from time to time sits in the pan, and sometimes goes through the movements of scrabbling etc. without material there. Also, during the very early stages of nest-building, when gathering often occurs without completion of the nest-building sequence (see below), the female also sometimes sits without previous gathering.

(b) Observations of birds gathering or carrying indicate that the change from gathering to carrying or carrying to sitting does not depend solely on the external stimulus. Thus a burst of active gathering may last over 100 secs., and low intensity gathering even longer than this, even though material is plentiful. On the other hand, when gathering actively the female may merely snatch material from the floor and fly off with it at once. Further, many gathering bouts do not lead to carrying, even though material is plentiful, and many carrying bouts do not lead to placing—though such incomplete sequences are less common when building activity is frequent (Table 10).

Thus the occurrence of carrying and sitting does not depend solely on stimuli resulting from the previous activity : internal factors also are involved. The positive correlations between the times spent in the various activities therefore suggest that they share causal factors.

However the correlations, although consistently positive, are by no means absolute. The correlation coefficient between the total times spent in carrying and sitting is reasonably high (mean, calculated by the z transformation, Fisher & Yates, 1938, was 0·72), but that between gathering and carrying is lower (mean 0·57). Further, the correlation coefficients are even lower if data from incomplete preliminary nesting cycles are included : thus at Cage 19/56 the correlation between gathering and carrying was 0·61 ($N=10$) for the period immediately before egg-laying, but 0·32 ($N=38$) when earlier data are included.

It seemed possible that the correlation would have been higher if gathering and carrying had been treated as one activity. The observational criterion of the change-over from gathering to carrying was merely that the bird left the floor of the cage, and thus perhaps arbitrary as far as the bird was concerned. However, the third column in Table 8 shows the correlation coefficients between the total of gathering and carrying and the total time sitting. At two nests the correlation coefficient is better than either of the two previous figures, but the improvement is not consistent (mean by z transformation, +0·69).

In the following paragraphs an attempt is made to elucidate this further by studying first the relations between the total times of each activity and other characteristics of building behaviour, and then the variation in the bout lengths of each activity.

(b) *Behavioural measures of building activity*

Although the positive correlations in Table 8 suggest similarities in the motivational bases of gathering, carrying and sitting, we cannot expect any behavioural characteristic to change precisely in parallel with any motivational

TABLE 9

Relation between number of placings and total time spent building. Figures indicate number of watches in each category. Data from birds with material present for watch only.

No. of placings Total time building	0	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	>50
0–100	9											
101–200	5	2										
201–300	3											
301–400	4											
401–500	5	3										
501–600			1									
601–700	1	3										
701–800	1	1	3									
801–900	1	3	2		1							
901–1000	1	1	3									
1001–1100			2	2	2	1						
1101–1200		2	1	2	1		1					
1201–1300		1	1	3	2	2	2	1		1		1
1301–1400				2	5	2	2	1	1	1		2
1401–1500		1	1	1	3	6	1	3		2		3
1501–1600					1	7	6	4	2	2	2	
1601–1700			2	1	1	1	2	1	2			
1701–1800				1		2	2	1				

factor or group of factors which they share. Many features of nest-building will vary with such factors, but not in a simple fashion. However, by selecting certain characteristics and studying the inter-relations between them, it is possible to gain some insight into the structure of the behaviour.

The two characteristics chosen for study were the total time spent building in each watch (i.e. the sum of the total times of gathering, carrying and sitting), which can be regarded as a measure of the probability of the bird being occupied in building in a given time interval ; and the number of placings in the watch, which is of course a measure of the effectiveness of the behaviour. The former is a measure of duration, the latter of frequency : neither takes account of the intensity with which the behaviour is performed (Russell *et al.*, 1954 ; van Iersel, 1953).

The relation between these two measures is shown in Table 9, which is based on watches in which material was available only for half an hour daily. Increase in the total time spent building is, in general, accompanied by an increase in the number of placings, but the correlation is by no means complete. The departure from complete correlation is due principally to two factors :

(i) At low values of the total time building, the increase in the number of placings is slow. Naturally gathering and carrying can occur without placing, but not vice versa ; the sequence with which the activities appear as the reproductive season advances suggest that gathering, carrying and sitting/placing require successively higher values of the internal factors common to all nest-building behaviour (see also p. 19).

(ii) At high values of the total time, the range in the number of placings is large, some watches with few placings having a high total time building. In such watches, with few placings yet a high total time building, the latter is due to relatively long bouts of gathering, carrying and sitting. In these long bouts the female's behaviour is dilatory ; gathering, for instance, consists largely of hopping to and fro looking at the material, with only rare pecks at it. Further, Table 10 shows that (a) nest-building sequences are more often incomplete (i.e. gathering not followed by carrying or carrying not followed by sitting) and (b) nest-building behaviour is more often succeeded by non-reproductive behaviour, after long bouts than after short ones. These facts show that a high total time of building per half hour is not necessarily associated with great vigour or effectiveness of the behaviour itself. A high number of placings, on the other hand, necessarily precludes dilatoriness in gathering and carrying and involves the completion of a large number of building sequences.

We can thus conclude that these two characteristics of building behaviour are not fully correlated with each other, the departures being due in part to differences between the strengths of internal factors necessary for the various building activities, and in part to the complex relation between the intensity of the behaviour and the bout lengths. These are considered further below.

It is possible that total time building would be better correlated with the number of placings if the watches were longer—watches with few placings but a high total time building might have shown a relatively lower figure for the latter if they had been continued to include the long feeding bouts, which probably occurred just after the watch was over. As placings become more frequent,

less time is spent in feeding and preening (Table 11) and building bout-lengths become shorter (Fig. 6), so that thirty-minute watches are adequate to indicate building activity.

TABLE 10

Variation in frequency of incomplete building sequences (i.e. gathering not followed by carrying or carrying not followed by placing) and of temporary gaps in building behaviour (i.e building followed by feeding, preening or a gap of more than 20 secs.), with bout lengths of preceding building activity.

		Bout length (secs.)							
		1–2	3—4	5–8	9–16	17–32	33–64	65–128	129–356
Gathering	Number of bouts	8	136	597	1042	877	467	152	30
	% not followed by carrying	(13)	1	3	6	12	19	29	47
	% not followed by building	(13)	1	1	4	7	11	21	33
Carrying	Number of bouts	332	850	775	661	394	172	47	8
	% not followed by placing	2	5	19	24	35	31	53	50
	% not followed by building	0	0	2	3	6	5	19	13
	% followed immediately by gathering	1	2	10	12	16	18	24	—
Sitting	Number of bouts	4	127	423	510	368	175	103	25
	% not followed by building	0	4	3	5	7	7	14	(4)

TABLE 11

Variation in occurrence of maintenance activities as building activity increases.

No. of placings per watch	No. of 30-min. watches	Percentage of watches in which fed	Mean total time feeding per watch (secs.)	Percentage of watches in which preened	Mean total time preening per watch (secs.)
1–5	43	100	345	72	126
10–15	39	93	115	38	18
>20	59	37	21	7	2

(c) *Relation between building activity and total time in each constituent activity*

We can now examine the relations between the total times spent in each constituent activity and the two characteristics of building behaviour discussed in the preceding section.

In Fig. 3 are plotted the mean total times spent gathering, carrying and sitting (building) in each watch, against the total time spent building in 100-sec. intervals : each point on the graphs is the result of plotting the mean times for each such interval. Each point on the graph is based on about ten watches, though the number is not the same in each case.

The crosses and continuous lines refer to fourteen birds who had material only for the duration of the half-hour watch, the circles and discontinuous lines for nine pairs which had material continuously (for differences between these two, see p. 44). The curves are not fitted.

In Fig. 4 the mean total times spent gathering, carrying and sitting (building) have been plotted against the number of placings, the watches being grouped according to the number of placings in intervals of five. Here the points are less regularly placed on the graph, and there was no significant difference between the birds which had material continuously and those which had it for the duration of the watch only ; only the latter are shown in the figure.

In both figures the total time spent gathering increases up to a maximum of c. 650 secs., though it falls again at high total building times in Fig. 3 ; the maximum is reached more rapidly in Fig. 4 than in Fig. 3. The total time spent carrying increases in both cases, the increase being positively accelerated in Fig. 3 and negatively in Fig. 4. Again, there appears to be a fall in the total time carrying at high total times of building.

The total time sitting increases in both cases, the increase being positively accelerated in Fig. 3 and initially fairly steady in Fig. 4. This time the total time sitting falls off at high total numbers of placings, but continues to increase with high total times of building.

Thus although Figs. 3 and 4 show that, in a general way, the total times spent gathering, carrying and sitting increase with increase in the total time building or total number of placings, the precise shape of the graph is different for each activity. This, of course, is an aspect of the incompleteness of the correlations in Table 8.

The differences between Figs. 3 and 4 are partly due to a difference in scaling along the abscissa—thus the figure for 0 placings includes much of the data for 0–500 secs. total time building (see Table 9). The other differences between Figs. 3 and 4 lie mainly in the figures for high total times of building or high numbers of placings, and can be partially understood as follows :

(i) The decrease in the total times of gathering and carrying at high total times building can be regarded as an arithmetical necessity of the very high total time sitting. Furthermore, as shown in Table 9, these data depend largely on watches in which the number of placings was small, and the number of gathering and carrying bouts was therefore smaller than at rather lower building times.

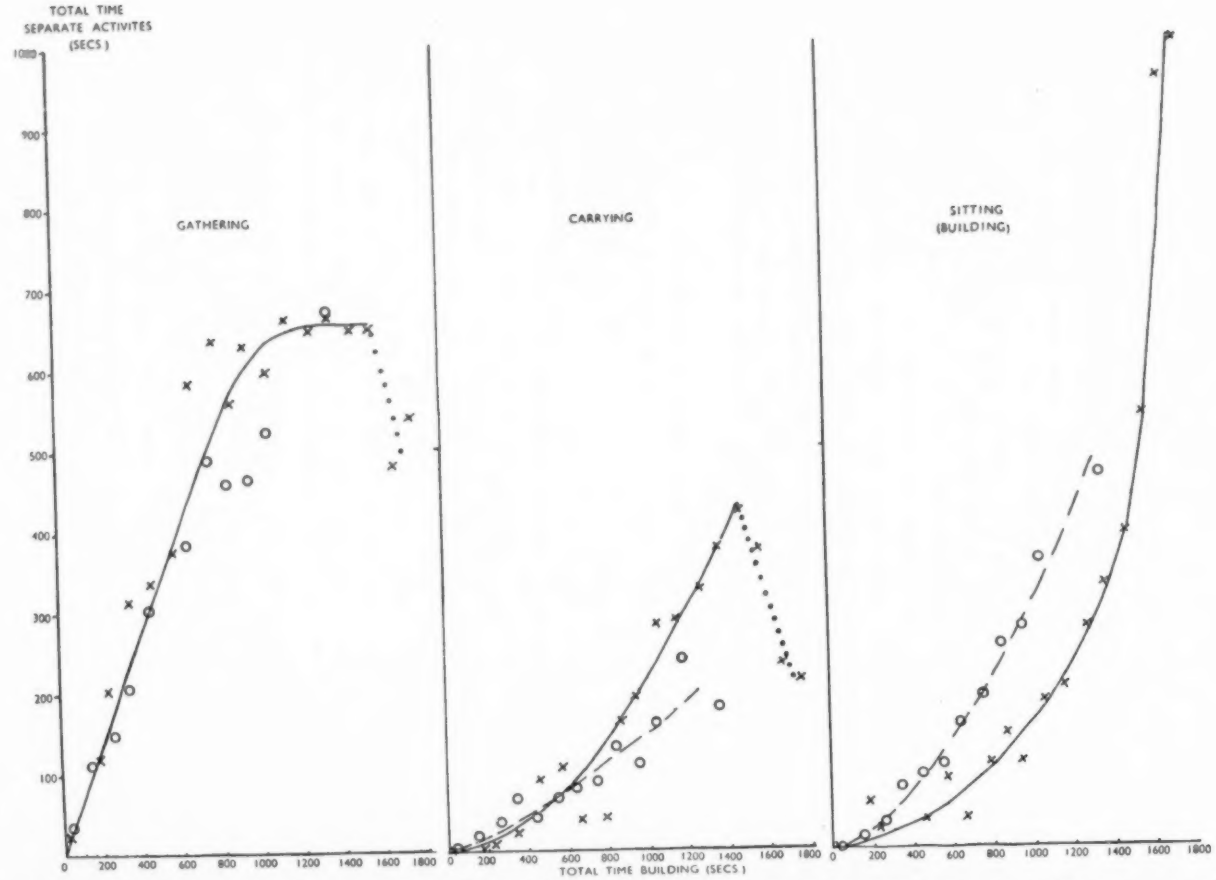


Fig. 3.—Changes in mean total times spent gathering, carrying and sitting (building) with increase in total time spent building. x material during watch only. o material continuously present.

Fig.

pa
sit
of
in

fre
the
of
rel
and
for

the
adv
the
diff

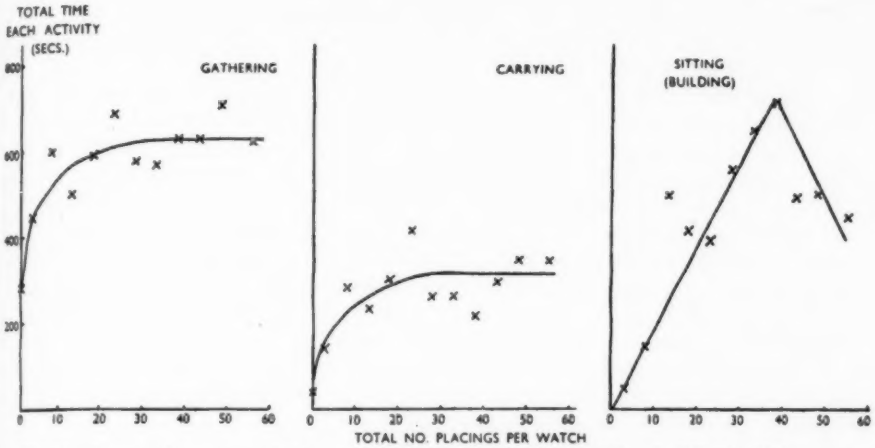


Fig. 4.—Changes in mean total times spent gathering, carrying and sitting (building) with increase in number of placings per watch.

(ii) The decrease in the total time sitting at high number of placings is partially due to an increase in the number of placings which do not involve sitting relative to the number which do. The relation between the number of placings and the percentage of them which do not involve sitting, shown in Table 12, is complex, but does involve a great increase at high placing

TABLE 12

Relation between number of placings and proportion of these which did not involve sitting.

	Number of placings					
	1–10	11–20	21–30	31–40	41–50	>50
Total number of placings	160	407	811	588	343	386
% placing without sitting	28	30	36	26	18	58

frequencies. This, however, is unlikely to be important in the reduction of the total time sitting at placing frequencies of 40–50, when the proportion of placings without sittings is low. Another factor is the reduction in the relative number of long sitting bouts at high placing frequencies (see below, and Figs. 5 and 6) : the reduction in mean bout length more than compensates for the increase in the number of bouts.

Figures 3 and 4 also illustrate another point. We have already seen that the successive appearance of gathering, carrying and sitting as the season advances suggests that these activities require successively higher values of the common internal factors for nest-building behaviour. Such threshold differences are also indicated here. In Fig. 4 the time spent in gathering is

Fig. 3.—Changes in mean total times spent gathering, carrying and sitting (building) with increase in total time spent building. × material during watch only. ○ material continuously present.

already considerable when the time spent in sitting is zero. In Fig. 3 the total time gathering increases initially more rapidly than that of carrying, which in turn increases more rapidly than that of sitting.

In summary, then, the total times spent gathering, carrying and sitting differ from each other in the manner in which they vary with either total time building or number of placings per watch. Figures 3 and 4 illustrate, in fact, the manner in which the correlations between them fall short of 1·0 (Table 8). The differences are due in part to threshold differences (p. 19), and in part to differences between the relations of the total times in the constituent activities to the characteristics of building activity used (p. 17) : these may in their turn be related—i.e. those same conditions which determine threshold differences could also influence the shapes of the graphs, but on this point there is no evidence.

Figures 3 and 4 illustrate the difficulties involved in the use of a concept such as " drive " in an analysis of this type. To be valuable, a " drive " variable would have to be quantifiable in terms of dependent or independent variables or both. Since the dependent variables are not fully correlated, their use to assess " drive " would inevitably depend on arbitrary decisions as to which variable is most suitable. It is also unlikely that " drive " could be related satisfactorily to independent variables (e.g. hormones) since the lack of correlation between nest-building activity and the proportion of feathers brought to the nest (see Fig. 2 and Sections 7 and 9) suggests that the hormonal basis is complex. The view that the concept of a " nest-building drive " is not useful in this context is, however, not incompatible with the view that the various nest-building activities share common internal factors ; nor, of course, does it imply that a " drive " variable is not useful in other types of analysis.

(d) *Relation between building activity and bout lengths of the constituent activities*

The change from gathering to carrying or carrying to sitting does not depend solely on the external stimulus (p. 13). It is therefore necessary to look for internal changes influencing the switch-over from one activity to the next.

As shown in Fig. 1, the mean bout lengths of the various activities change throughout the nest-building cycle, and tend to decrease towards the date of egg-laying. Figure 5 shows the changes in the frequency distribution of bout lengths of gathering, carrying and sitting with increase in the number of placings. The median bout lengths are shown in Fig. 6. At all placing frequencies the bout lengths of each activity are highly variable, but, as the placing frequency increases, the median bout lengths increase to a maximum and then decrease again. The decrease is due to the peak on the frequency distribution diagram occurring at progressively lower bout length values, and also to its becoming more marked—that is, very long bouts become rare.*

* There is an apparent discrepancy between Figs. 6 and 10, in that the graph of *mean* sitting bout length against number of sitting bouts shown in the latter shows no initial increase. This is due to two factors : (a) Because some placings do not lead to sitting, the abscissa of the graphs are not strictly comparable (Table 12) ; (b) In one case mean bout lengths are shown, in the other medians.

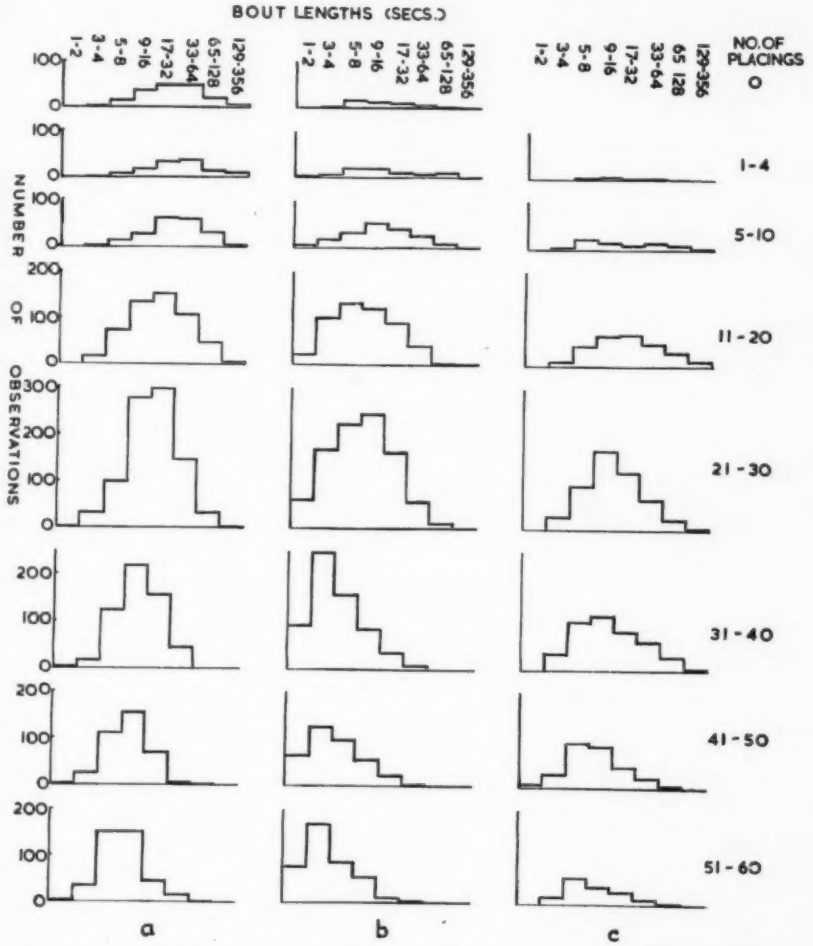


Fig. 5.—Frequency distribution of bout lengths of gathering, carrying and sitting (building) at different numbers of placings. Birds with material for duration of watch only.

The changes in bout lengths with increase in the total time of building were also analysed. It was clear, however, that this involved grouping together watches which, although they had similar total times of building, were markedly heterogeneous in the means and medians of their bout lengths. Only certain general conclusions were possible :

(a) Gathering bouts at first tended to increase in length with increase in the total time spent building, up to a maximum at about 700 secs., and then fell off.

(b) Carrying bout lengths also increased to a maximum at about the same point, and then they became slightly but significantly shorter.

(c) The bout lengths of sitting (building) are even more variable than those of gathering and carrying, but the analysis indicated an initial increase to a maximum at c.900 secs. Between 700 and 1500 secs. the meant sitting bout length decreased slightly and the median markedly—

the difference being due to a small number of very long bouts. At very high building times, which are not reached under normal conditions, the average bout length of sitting bouts increases again. As discussed above, however (p. 19) the watches with very high total building times involved few placings.

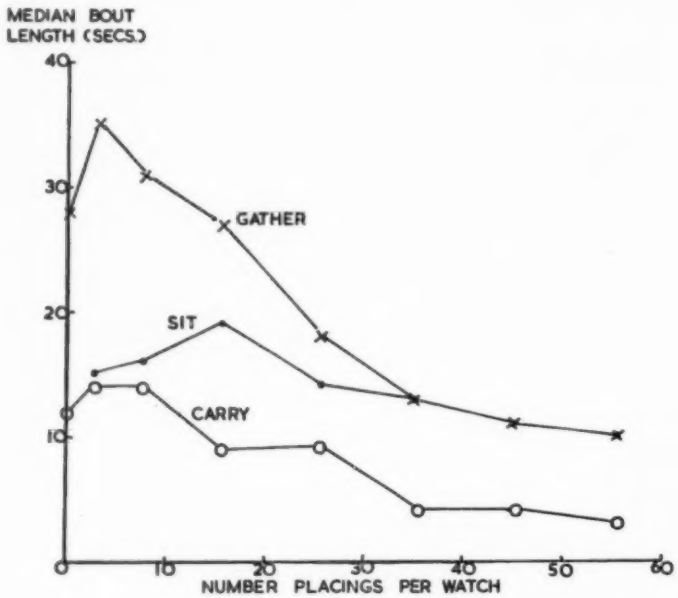


Fig. 6.—Median bout lengths of gathering, carrying and sitting at different values of the number of placings. Birds with material during the daily watches only.

The shortening of gathering and carrying bouts when building is vigorous shows that the plateaux reached by the curves of total times gathering and carrying plotted against the number of placings (Fig. 4) are due to a balance of two effects—increase in the number of bouts compensating for the decrease in their mean length. In the case of sitting, the shortening of the mean bout lengths at high total times of building is less, so that the total time sitting continues to increase : at high numbers of placings, however, the shortening of the bouts, and the increase in the number of placings without sitting, more than compensates for the increase in the number of building sequences.

The peaks in the medians of gathering, carrying and sitting occur at successively higher values of the number of placings—that is, the peak bout lengths of the lower threshold activities are reached earlier. This, of course, is another factor operating against complete correlation between the total times in these activities (Table 8). In fact the gathering bout lengths tend to be maximal on the day where carrying first starts, and those of carrying tend to be maximal when sitting first starts. This can be demonstrated in another way. Data for the two days preceding and three days succeeding the first appearance of carrying and sitting for eight nests were analysed as follows.

At each nest the days were ranked according to the mean length of the gathering (or carrying) bouts—six for the day when the bouts were longest, five for the next, and so on. The mean ranking scores for all nests is shown in Table 13,

TABLE 13

Mean ranking scores for lengths of gathering/carrying bouts around the time when carrying/sitting started—for explanation of system of scoring, see text. Day 0 is day when carrying/sitting started.

	Day					
	−2	−1	0	+1	+2	+3
Index of relative gathering bout lengths	1·7	3·8	4·6	4·3	2·7	3·1
Index of relative carrying bout lengths	2·4	3·6	4·3	3·5	2·6	2·5

where it will be seen that the score for the first day of carrying (in the case of the gathering bouts) or sitting (in the case of carrying) was greatest. (For estimating the start of carrying, watches in which only a single carrying bout was recorded, and which were followed on the next day by a watch containing no carrying, were ignored).

In summary : (i) the bout lengths of each activity at first increase with increase in the number of placings, and then decrease. This enables the shapes of the curves in Fig. 4 to be understood. (ii) the peak median bout lengths of gathering, carrying and building occur at successively higher values of building activity, and (iii) the peak median bout lengths of gathering and carrying occur just when carrying and sitting respectively first appear. We have already seen that long bouts often consist of behaviour of relatively low intensity—dilatory gathering and carrying which does not consist of a flight straight to the nest, but of flights to and fro with perching in between. Thus increase in the number of placings is associated with more intense building behaviour and shorter bout lengths—i.e. a more rapid change-over from one activity to the next.

(e) *The relation between the successive bout lengths in a building sequence*

Since the building activities appear to depend on common internal factors (p. 12), we would expect a relation between the bout lengths of the successive activities in individual building sequences. This relation could not be a precise one, however, since the peak bout lengths of the different activities do not occur at the same value of the number of placings per watch (Fig. 6).

Table 14 shows the median lengths of carrying bouts which followed gathering bouts of various lengths. This table, together with Tables 15 and 16, is based on analyses of nestings during which material was available for the half hour daily watch only : all watches in which incubation occurred were excluded, and in the remaining watches only those gathering-carrying-sitting

TABLE 14

Relation between length of carrying bout and length of previous gathering bout. Based on fifteen nests.

		Bout length of previous gathering bout (secs.)					
		3–4	5–8	9–16	17–32	33–64	65–128
Carrying bouts not followed by building	N	3	10	9	16	12	2
	Median length	(6)	6·5	10	7·5	12·5	(17)
Carrying bouts followed by gathering	N	—	10	33	24	15	4
	Median length	—	5·5	9·5	8	10	18
Carrying bouts followed by placing and/or sitting	N	34	87	229	196	92	22
	Median length	3	6	6	6	8·5	6

sequences which were preceded by a gap of two or more seconds from the previous sequence, and which were not interrupted by activities of the male, were included.

Considering first those carrying bouts which did not lead to sitting or placing, Table 14 shows that the longer the previous gathering bout, the longer the median carrying bout. When the carrying does lead to placing or sitting, however, the increase in the median bout length is only slight.

Table 14 also shows that carrying bouts which do lead to placing are shorter than those which do not : thus carrying can be interrupted by placing when the carrying tendency has not fallen to threshold (see pp. 25–7). The same point is also indicated in Table 10, which shows that longer bouts of carrying are followed by a break in the nest-building sequence more often than are short ones. On the other hand, carrying bouts interrupted by gathering are of a similar length to those followed by no building behaviour, suggesting that carrying cannot be interrupted by gathering unless its motivation has fallen to near threshold.

TABLE 15

Relation between length of sitting bout and length of previous carrying bout. Based on fifteen nests.

		Bout length of previous carrying bout (secs.)						
		1–2	3–4	5–8	9–16	17–32	33–64	65–129
Sitting bout	N	41	142	114	114	74	28	3
	Median length	15	15	15	16	17	14	14

Table 15 shows that the length of carrying bouts is not related to the median length of the following sitting bout. There is, however, a relation between the length of a gathering bout and the length of the following sitting bout. This is shown in Table 16, the sitting bouts being divided into those which were followed by an interval of five secs. or less before the next gathering bout, and those followed by a longer interval. In both cases the median length of sitting bouts increases with the length of the previous gathering bout. Those sitting bouts followed almost immediately by gathering are shorter than those which are not (cf. Table 10 and p. 15), suggesting that sitting can be interrupted by gathering before the tendency to sit has fallen to its normal threshold.

TABLE 16

Relation between length of sitting bouts and length of previous gathering bout. Based on fifteen nests.

		Length of previous gathering bout (secs.)							
		1–2	3–4	5–8	9–16	17–32	33–64	65–128	129–356
Sitting followed by interval of <5 secs.	N	—	9	60	184	184	71	8	—
	Median sitting	—	5	12	16	23	28	31	—
Sitting followed by interval of >5 secs.	N	2	6	33	66	69	38	9	3
	Median sitting	(18)	15	20	31	29	34	37	(25)

Thus we may say that there is a tendency for the bout lengths of the various activities to increase together, except for carrying bouts followed by sitting or placing, whose median length is almost independent of the length of the previous gathering bout or following sitting bout. Further, each activity can be interrupted by that which normally follows it.

(f) *The appetitive-consummatory behaviour dichotomy*

We have seen that the bout lengths not only of gathering and carrying, but also of sitting (building) behaviour, decrease when building activity is vigorous.

Nest-building seems to differ in this respect from some other behaviour sequences which have been studied. Thus van Iersel (1953) showed that as the time spent in parental fanning by the Three-spined Stickleback increased, the bout lengths increased ; and Bastock & Manning (1955) showed that the more *Drosophila* males court, the longer the bout length of the highest threshold courting activity. The hoarding and nest-building of rodents, however, is probably similar to the nest-building of canaries, increase in frequency of trips being associated with a decrease in bout-lengths (Verplanck & Berry, pers. comm.).

This shortening of sitting bouts usually means that the motor patterns of scrabbling etc. are performed less often in each bout. Although the interval between scrabblings tends to decrease with the rate of building (p. 29), this does not compensate for the reduction in the length of bouts, and the

number of scrabblings per bout decreases with the number of bouts per watch. The data from different nestings were consistent in trend, but the rate of decrease varied greatly : some examples are shown in Fig. 7.

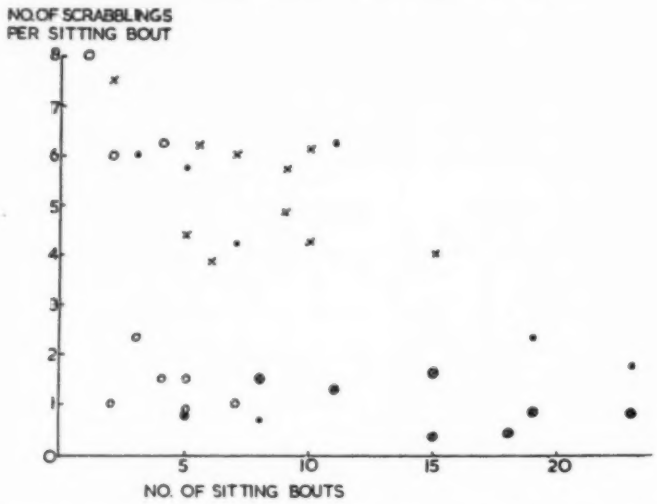


Fig. 7.—Changes in number of scrabblings per bout with frequency of placings. Each symbol refers to a different nesting.

This shortening of the sitting bouts is due to the bird leaving the nest to gather, and thus to start a new building sequence, and not to the interpolation of maintenance activities, as is shown by the following facts :

(i) Maintenance activities become quite rare when sitting (building) is frequent, as shown by the sample analyses for watches in which the bout frequencies were 1–5, 10–15 and >20 in Table 11.

(ii) In those watches containing 10–15 sitting (building) bouts, periods of maintenance activities followed incomplete building sequences (i.e. those not leading to placing or sitting) in fifty out of 103 cases (i.e.c. 49 per cent). Since less than 25 per cent of carrying bouts are incomplete at these building intensities (Table 10), maintenance activities are relatively more frequent after incomplete sequences than after complete ones, and thus cannot play any large part in interrupting sitting bouts.

(iii) Those sitting bouts which are not immediately followed by other building activities are longer than those which are. Thus Table 10 shows that the proportion of sitting bouts not followed by building increases with sitting bout length, and Table 16 shows that for each range of gathering bout lengths, the median sitting bout length is longer when building does not follow within five secs.

The distinction between " precurrent " or " appetitive " and " consummatory " behaviour was originally due to Sherrington (1906) and Craig (1918). As used now, this dichotomy often rests on behavioural

characteristics which are not correlated with each other. Thus consummatory behaviour is said both to come at the end of the behaviour sequence, and to produce a decreased tendency to perform any part of the sequence. In many cases the performance of the final pattern in a behaviour sequence is indeed associated with such an inhibitory effect. Thus in the Three-spined Stickleback fertilisation is associated with a decreased tendency to show sexual behaviour (van Iersel, 1953). Similarly a Chaffinch which has ejaculated onto a model of a soliciting female will not court the model again until a time interval has elapsed : in neither of these cases, however, is the mechanism underlying the refractoriness understood. In the case of nest-building, on the other hand, the behaviour which comes at the end of the sequence, namely sitting, produces no such dramatic decrease in the tendency to perform all nest-building activities, for sitting may be *interrupted* by gathering. It must thus be emphasised that the dichotomy between appetitive and consummatory behaviour, while useful for purposes of description and classification, is not fundamental—so that generalisations about the relationships between their respective " drives " are unlikely to be fruitful. Although the observations cited in this paper indicate that the " appetitive " gathering and carrying, and the sequence-terminating sitting, share motivational factors, this motivation is not " used up " by the performance of the latter.

Another at least partial explanation of the decrease in bout lengths of all building activities with increasing building activity can, however, be suggested. Suppose that the performance of *each* activity (the relevant aspect or consequence of performance not being specified) is accompanied by a self-suppressing effect, i.e. a reduction in the tendency to continue or repeat that activity relative to the tendency for other related activities. (It may, of course, also cause a decrease in the tendency for the related activities, but that is not relevant here). This is, of course, a concept related to Hull's I_R, though it is not specified here whether the change in relative tendencies is due to the inhibition of one activity or the excitation of another. Then when the bird is gathering, the tendency to continue gathering is progressively reduced until it is lower than the tendency to carry, and the bird will then carry. (An inertia effect, or time lag in the effectiveness of the suppression, must of course also be postulated, or the bird would stop as soon as it started). Carrying will continue until the carrying tendency is less than the tendency to sit, and the bird will then sit. While the bird is sitting, the tendency to continue sitting will decrease and the suppressing effect on gathering will be dissipated, so that the bird may leave the nest to gather.

If we further suppose that the suppressing effect accumulates more rapidly with increasing vigour of performance, and that the latter depends on common causal factors shared by all building activities, then the increase in the bout lengths of carrying and sitting with increase in the previous gathering bout (Tables 14 to 16) can be understood.

Causal relationships of this type would be in harmony with the principal characteristics of nest-building behaviour noted earlier in this section, at least in a qualitative fashion. The precise mechanisms underlying the relationships which have been demonstrated are, however, still not specified,

and a number of ambiguities remain. Thus shortening of sitting bouts with increasing building activity (Fig. 6) could be due to the more vigorous sitting (building) leading to a more rapidly decreasing tendency to continue sitting; or to a more rapid dissipation of the suppressing effect on gathering so that it can interrupt sitting more quickly, or both. Similarly, the increase in the median sitting bout length with the length of the previous gathering bout could be due to less vigorous activity and thus a slower accumulation of the suppressing effect on both gathering and carrying. Alternatively it could be due to a longer gathering bout being associated with the accumulation of a greater suppressing effect, which therefore takes longer to dissipate.

Such ambiguities remain, and this analysis is to be regarded as preliminary only. It is, however, sufficient to show that the relationships between gathering, carrying and sitting (building) cannot be understood in terms of a unitary "nest-building drive", or in terms of the appetitive/consummatory behaviour dichotomy, but can be analysed in terms of concepts such as common causal factors, threshold differences, and self-suppressing effects consequent upon performance, which have a wide applicability in other aspects of behaviour study. Each of these concepts, of course, requires further analysis.

6. VARIATIONS IN THE FREQUENCY OF NEST-BUILDING MOVEMENTS

(a) *General*

A detailed study of the variations in frequency of scrabbling, turning, etc. has not yet been made. Although the movements themselves are stereotyped, the relative frequency with which they are performed varies between individuals (Table 17). It is to these differences that the variations between nests in compactness, solidity, tidyness etc. are largely due.

TABLE 17

Individual variations in the frequency of nest-building movements. Records refer to watches with normal nest-pan during the twelve days before egg laying, the birds having material during the watch only.

Nest No.	No. of scrabblings observed	Mean interval between scrabbles	Ratio of no. of turns to no. of scrabbles	Ratio of no. of pulls to no. of scrabbles
35	281	12·0	·78	2·0
27	153	18·2	·87	3·1
17	55	33·3	·93	4·8
11	58	18·4	·62	3·8
10	16	34·0	1·0	8·8

The frequency of pulling and weaving depends largely on the external stimulus situation—so long as pieces of grass are protruding, the female is likely to pull them in. The frequencies of scrabbling and turning fluctuate roughly together—most birds scrabble more often than they turn—but the

ratio of the number of scrabbles to the number of turns remains roughly constant in each individual. Normally a female scrabbles several times and then turns, pulls several times, scrabbles, turns, and so on.

(b) *Variations in frequency of scrabbling*

Figure 8 shows, for four nests, the mean interval between scrabblings, calculated by the total time sitting (building) per watch divided by the total number of scrabblings per watch, during the period preceding the laying of the first egg. These include females 11 and 12/56 whose building activity

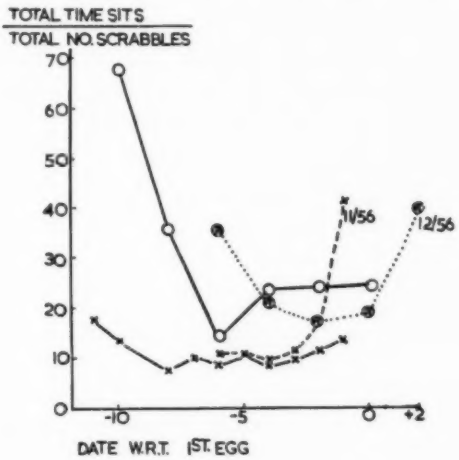


Fig. 8.—Relation between mean interval between scrabblings and date with reference to first egg at four nests.

is shown in Fig. 1 a and b. It will be seen that the frequency of scrabbling is greatest during the period of active building, and tends to decrease at the beginning and end of the cycle when building activity is lowered. In many cases, however, the frequency of scrabbling while sitting is remarkably constant. Thus at Cage 19/56, whose building activity is indicated at the top of Fig. 2, the mean interval between scrabblings was estimated on twenty-five days during the period between Day –34 and Day 0 : it lay always between 17·4 and 6·3. Further, the longer mean intervals occurred only in the few days before egg laying, and in the period Day –34 to Day –4 the mean interval always lay between 12·9 and 6·3, except for Day –23 when it was 15·4.

The frequency of scrabbling also varies with the nature of the nest-pan which is present. Table 18 shows the effect on the mean interval between scrabbles of substituting the small grass nest-pan or the small bare nest-pan for the normal bare nest-pan on alternate days. The comparisons are based on counts of scrabblings made during some of the experiments described in Sections 7 and 9, and the analysis depends on a similar grouping of the days

in triplets. There is a significant increase in the frequency of scrabbling with the small nest-pans which appears to be an immediate response to the changed stimulus situation.

TABLE 18

Effect of nest-pan on frequency of scrabbling. N refers to number of triplets on which comparison in based.

Pan B	Mean Total time sitting / No. scrabbles in Pan A	Mean Total time sitting / No. scrabbles in Pan B	N	Diff. significant with P ⩽
Small grass nest substituted 24 hours previously	33·4	11·1	20	0·001
Small hard pan substituted just before	26·3	13·5	27	0·01
Small hard pan substituted 24 hours previously	34·3	17·1	17	0·05

7. CONTROL OF THE CESSATION OF NEST-BUILDING

(a) *General*

This section is concerned with the factors which control the waning of nest-building around the time at which the first egg is laid. The increase in nest-building early in the cycle is presumably due to an internal change, for the external situation is constant. When the canary is allowed to build a nest, however, the subsequent waning could be due to internal factors—perhaps further changes in the hormonal state—or to external factors—depending on stimuli presented by the nearly finished nest—or both.

(b) *Internal factors*

Sixteen females were placed in separate cages, each with a male and a plentiful supply of nest material. Each day all the material which had been carried to the nest-pan was removed, so that the female was never allowed to build a complete nest. Nevertheless, building activity fell off at about the same time as with females whose nests were undisturbed. Some examples of this are shown in Fig. 2. The material removed from the nest pan was weighed each day and the day of peak building activity assessed for each bird. The mean peak day for all birds whose nests were removed daily (–3·0, N=16) does not differ significantly from that for females whose nests were undisturbed (–3·2). In both cases building activity virtually ceased in nearly all pairs by a day or two after the first egg was laid.

In spite of the daily removal of nest material from the nest-pan, these birds were able to accumulate several grams of material each day, and stimuli from these nests, daily partially completed, could have had some inhibitory

influence on building. However, with those pairs which were allowed nest material for half an hour a day only, the building activity fell off in the same way around the date of the first egg. The number of visits to the nest with material during the half hour watch was counted each day : the initial onset, peak and waning of building activity are indicated in Table 4. The peak day (-2·2) was later than that for birds under normal conditions, the difference being significant ($P<0·05$).

Thus under these conditions the peak of the building activity is delayed. This may be due to the absence of some factor present in normal building, when it causes a decrease in building activity earlier (relative to the laying of the first egg) then the decrease which occurs when material is present for half an hour a day only. This factor could be related either to the actual performance of nest-building activities, or to the nest which normally results from them, or to both. There is no evidence concerning the former : the importance of the latter is demonstrated below.

(c) *External factors*

With six females the weight of material, brought to the nest during the ten days preceding the laying of the first egg when the nest was undisturbed, was compared with the total weight brought in a similar period at another nesting (earlier in the season in three cases and later in three cases) at which the nest was removed daily. In every case the total weight of material brought was greater when the nest was removed daily, the means being 5·2 gms. for undisturbed nests and 13·5 gms. for the others.

When data from four other females who were allowed to build undisturbed and six whose nests were removed daily are included, the means are 6·1 gms. for undisturbed nests and 19·0 gms. for the others : these differ significantly. It is thus clear that the presence of the nest already built depresses the amount of material brought. That this is due to a reduction in nest-building activity is indicated by the experiments quoted below.

In a further series of experiments some of the characteristics of the nest responsible for this reduction in nest-building activity were investigated. Females were confined with males but were provided with nest material for the duration of the half hour watch each day only, at the end of which all material was removed both from the nest-pan and from the floor of the cage. A normal plastic nest-pan (Pan A) was present in the cage throughout the settling down period, and also on every alternate day during the experimental period. On the intervening days a different nest-pan was substituted. This pan (Pan B) differed in size or texture or both from the normal one. Thus while the normal pan was 10·5 cms. in diameter and 4·5 cms. deep, the substituted pans were as follows :

(i) Small hard pans. These consisted of a normal nest-pan partially filled with plaster of paris so that the cup was only 7·0 cms. in diameter and 3·5 cms. deep.

(ii) Normal-sized grass pans. These consisted of a wire netting frame lined with grass. The grass was tied in place with wire so that it was fairly compact and the internal dimensions were similar to those of the normal pan.

(iii) Small grass pans. Similar to the normal grass pan, but with internal dimensions similar to the small hard pan.

Further, in some cases Pan B was substituted for the normal pan immediately before the observation period, while in others it was substituted twenty-fours previously—i.e. immediately after the observation period with the normal pan (Pan A) on the previous day. In series involving grass pans, a small quantity of loose material was left on the floor of the cage at all times. This prevented the bird destroying the grass nest-pan, but was not sufficient to make any appreciable difference to the size of the pan if placed in it.

The data obtained from all these experiments were analysed as follows. Successive days' observations were grouped in trios in such a way that one trio consisted of observations on Pan A, then Pan B, then Pan A ; the next of observations on Pan B, then Pan A, then Pan B ; the next of Pan A, Pan B, Pan A, and so on. The mean of the number of times material was placed in the pan during the first and third days' observations of each trio was compared with the number of placings on the middle day. The difference gives a measure of the effect of substituting Pan B for Pan A. This difference was expressed as a percentage of the number of visits to Pan A—the latter being obtained either from the actual number of visits to Pan A on that day, or from the mean number of visits to Pan A on the first and third days. Since each day's observations were used in only one trio, the percentage differences obtained from successive trios are independent of each other.* The effect

TABLE 19

Percentage decrease in number of visits caused by substitution of various pans for normal hard pan (Pan A).

Pan B		Period since Pan B substituted for Pan A	No. of trios on which difference based	Mean decrease %	S.E.
Size	Texture				
Small	Grass	24 hrs.	28	47	8
Small	Grass	0 hrs.	12	33*	7
Normal	Grass	24 hrs.	31	25*	15
Small	Hard	24 hrs.	58	5	7
Small	Hard	0 hrs.	20	−9	9

* See text

of each type of Pan B was tested with at least four females. The mean difference from all trios for each type of substitution are shown in Table 19. It will be seen that :

(a) Substitution of the small grass pan twenty-four hours earlier produces a significant fall in the number of placings.

* Strictly speaking, since the relation between the number of placings and the date with reference to the first egg is not linear, a transformation should have been used. It was, however, not possible to find a satisfactory one. A logarithmic transformation similar to that used in Section 9 was adequate only if the latter half of each nesting cycle (i.e. the falling part of the building curve) was rejected. Some preliminary tests with such a transformation gave results similar to those obtained as described above.

(b) Substitution of this pan immediately before the watch also produced a fall in the number of placings. This may, however, have been due in part to the disturbance caused by the substitution or by the unfamiliar pan. (When the substitution was made twenty-four hours before the watch, the birds became equally familiar with both pans. The small grass pan differed in visual characteristics from the normal pan more than did the small hard pan and was therefore more likely to cause disturbance).

(c) None of the other substituted pans produced a significant fall. The results obtained with the normal sized grass pans were, however, variable between females. With two birds this pan produced a significant fall in the number of placings (66 per cent, SE=5). With six other females no effect was produced. These two exceptional females were rather larger than the rest, and this may explain their behaviour.

It thus seems that, under these conditions, both a grassy (or soft) texture and a reasonably small pan size relative to body size are necessary before building activity is reduced.

As a check on the result obtained with the small hard pan, four females provided with material continuously were given the normal hard pan and the small hard pan on alternate days. The small pan was substituted immediately after the watch on the normal one (i.e. twenty-four hours before the watch in which it figured). The material was removed from the nest-pan each day and weighed, and the resulting weights grouped in trios and analysed as above. The result of this experiment was similar to that in which the number of placings was used as the criterion. For the fifteen trios of observations available, the substitution of the small pan caused a decrease in the amount of material brought by 12 per cent, the standard error being 20.

(d) *Conclusions*

There is an internally governed waning in the building tendency around the time when the first egg is laid. This is internal in the sense of being independent of any change in the external stimulus situation, though it remains to be shown that external stimuli (e.g. those derived from the bare nest-pan) are not necessary. Two females kept in a round-bottomed cage which lacked any possible nest-site, who were never seen to perform the movements usually performed in the pan, showed what were probably cyclical fluctuations in the proportion of feathers which they carried about (cf. Fig. 2) : the results, however, were not conclusive.

It has also been shown that more material is brought if the nest is removed daily, and some of the stimuli from the nest which are normally involved in inhibiting nest-building have been investigated. This double control of the cessation of nest-building is probably general in other species—thus tits (e.g. *Parus major*) bring more material when nesting in large holes than in small ones, and build only small nests if the building is for some reason delayed until near the date of egg-laying (Hinde, 1952).

8. THE EFFECT OF THE NEST PAN ON SITTING BOUT LENGTH

Since stimuli from the uncompleted nest affect the building activity, they will also affect the various characteristics of the building sequence (e.g. the bout lengths of the constituent activities). These characteristics are interrelated, so it is difficult to tell which of the effects of a change in the stimuli

from the nest are primary. For this reason no detailed analysis has been attempted. Table 20, however, shows the effect of substituted nest-pans on

TABLE 20

Effect of change in size of nest-pan on total time sitting (building) and on bout length of sitting.

Substituted pan	No. of triplets available for comparison	No. of triplets in which total time sitting with substituted pan was less than with normal	No. of triplets in which mean bout length of sitting with substituted pan was greater than with normal
Small hard, just before	7	7	5
Small hard, 24 hrs. earlier	9	7	8
Small grass, 24 hrs. earlier	18	10	12
Normal grass, just before	16	16	2
Normal grass, 24 hrs. earlier	4	1	2

the length of sitting bouts. The data were obtained by analysing successive days' observations in triplets as described on p. 32 and suggest that :

(a) Substitution of the small pans causes a decrease in the total time of sitting and an increase in the mean bout length. These effects occur even when the second pan is substituted immediately before the watch.

(b) Substitution of the large pans causes a decrease in both total time and bout length.

The data obtained from substitutions just before the watch may, however, have been influenced by the effects of the disturbance, as noted on p. 33.

9. THE SELECTION OF NEST MATERIAL

(a) *General*

In all experiments discussed in this paper, the nest-material provided consisted of roughly equal volumes of dried grass and feathers. Although in any long observation period the female usually carried some of both to the nest, in undisturbed cycles the outside of the nest was built mainly of grass and the cup lined with feathers. The question of what controls the change-over from grass to feathers therefore arises. The factors could, of course, be internal, external, or both.

(b) *Internal factors*

A number of females were provided with material continuously, but the nest which they built was removed from the nest-pan daily. This material was divided into feathers and grass, each of which was weighed. The ratio of the weight of feathers brought to the total could then be calculated. Some

examples of the results obtained (selected by the completeness of the data, but not in any other way) are shown in Fig. 2. They show that, even when a complete nest is not built, the proportion of feathers brought to the nest increases as the cycle progresses. There are, however, great individual differences in the time when the change-over from bringing mostly grass to bringing mostly feathers occurred. The day when the weights of feathers and grass brought were equal were calculated in each case, and varied from Day −6·9 to +1·5—the mean for sixteen nests being Day −3·8. (This is almost the same as the mean of Day −3·7 obtained from five females whose nests were removed daily, divided into grass and feathers which were weighed separately, remade, and replaced.)

It is thus clear that there is an internally governed change in the selection of nest material—probably due to a hormonal change. Since the motor patterns used are essentially similar throughout nest-building, this internal change would seem to affect primarily the relative responsiveness to stimuli in the gathering phase of building.

(c) *External factors*

The influence of the partially completed nest on the proportion of feathers and grass brought was studied in the same way as its influence on the frequency of building (see Section 7). In brief, the females were provided with material for half an hour a day only, during which the building behaviour was recorded. The number of times that feathers or grass were placed in the nest-pan were counted—usually one or the other was carried, but the occasional visits with both were counted as being half of grass and half of feathers. The nature of the nest-pan was changed every other day in the manner described above (p. 31).

As before, the analysis depends on the grouping of successive days' observations in threes : a figure derived from the observations on the first and third days of the trio with one type of nest-pan is compared with a figure obtained on the second day with a different pan. The percentage of feathers changes in a roughly S-shaped curve with time over the course of a complete cycle : this, together with the difficulties inherent in the use of proportional figures directly, necessitated the use of a suitable transformation. Accordingly the

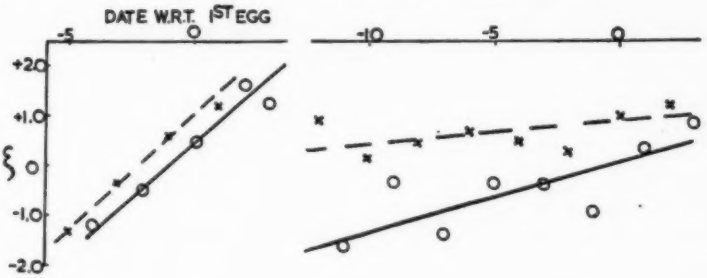


Fig. 9.—Relation between $\xi = \log_e \frac{r+\frac{1}{2}}{n-r+\frac{1}{2}}$ and date with reference to first egg at two nests. Continuous line—observations with Pan A. Discontinuous line—observations with Pan B.

change in the selection of material was measured by change in a quantity ξ where $\xi = \log_e \frac{r+\frac{1}{2}}{n-r+\frac{1}{2}}$

(r=number of visits with feathers n=total number of visits)

ξ was calculated for each day's observation, together with its theoretical variance (see Anscombe, 1946). If ξ is plotted against time for a normal uninterrupted cycle, the graph is a straight line (Fig. 9)—that is, roughly speaking, the ratio of the number of visits with feathers to the total number of visits is multiplied by a constant amount each day (see Table 22 and p. 37).

The effect of changing Pan B (see p. 31) for Pan A was calculated as follows:

(i) Successive days' observations were grouped in threes as before : observations of the first and third days of each triplet were with one pan, those on the second day with another.

(ii) $\xi = \log \frac{r+\frac{1}{2}}{n-r+\frac{1}{2}}$ was calculated for each day's observation, together with its theoretical variance.

(iii) The mean value of ξ was calculated for the first and third days of each group of three, together with its variance.

(iv) The difference between this mean and the actual value obtained on the second day was calculated, together with the variance of the difference. The difference was considered positive if ξ was greater with Pan B than with Pan A.

The results are summarised in Table 21—the figures referring to the number of differences, calculated as above, which were significantly greater, greater, less than and significantly less than zero. (Difference $> 2 \times$ Standard Error is

TABLE 21

Change in proportion of feathers (expressed as $\xi = \log \frac{r+\frac{1}{2}}{n-r+\frac{1}{2}}$ carried to Pan B compared to proportion to Pan A.

Pan B		Period since Pan B substituted for Pan A	Number of trios				Mean increase in ξ	S.E.
Size	Texture		Significantly greater	Greater but not significantly	Less but not significantly	Significantly less		
Small	Grass	24 hrs.	6	20	2	0	1·24	0·19
Small	Grass	0 hrs.	2	7	2	1	0·34	0·22
Normal	Grass	24 hrs.	11	12	8	0	1·18	0·24
Small	Hard	24 hrs.	15	34	9	0	0·85	0·06
Small	Hard	0 hrs.	1	14	4	1	0·47	0·15

taken as significant). The differences in each case indicate the effect of the substituted pan as compared with the standard Pan A. Table 21 also shows the weighted mean difference in ξ for each type of treatment for all experiments on each type of substituted pan.

The effect of a given substitution on ξ varies with the phase of the nesting cycle (see below, Fig. 9 and Table 22). Since the length of the nesting cycles of the various pairs could not be controlled, it was not possible to ensure that the trios with the different types of substitution were distributed in exactly the same manner over the nesting cycle. Further, there are individual differences between females in the effect of a given substitution (Table 22). The weighted mean differences in Table 21 thus cannot be used for a precise comparison of the effects of the different treatments, though they do provide a fairly reliable indication.

It will be seen that all types of substituted pan produced an increase in the proportion of feathers, though the grassy texture was apparently more effective than the smaller cup size. Although the results with the small hard pan show that reduction in the size of the cup is effective when not combined with a change in the texture, the small grassy pan was little more effective than the normal sized grassy one—perhaps because the effect of the latter was near maximal already.

The results may be compared with those in the previous section, where it was shown that a change in both texture and size was necessary to produce a fall in building activity. If only one of these characters is altered the nature of the material brought alters but the number of placings is unaffected—though of course more radical alterations than were involved with this series of experiments might have been effective.

The small grassy pan and the small hard pan were both effective even when substituted immediately before the watch, though the increase in ξ was not significant in the first case, and in both was significantly less than that produced when the substitution was made twenty-four hours before the watch.

In order to obtain a better indication of the length of time necessary for the small pan to cause an increase in the proportion of feathers, the data from two nests in which the small hard pan had been substituted immediately before the watch on alternate days were analysed by successive ten-minute periods. In both cases the mean value of ξ for the large pan for the first ten minutes (−2·07, +0·35) was smaller than that for the small pan in the same time interval (−1·66, +1·02). In one case the mean increase from the first to the third ten-minute interval of each watch was greater with the small pan (increase 1·05, v'nce = 0·06) than with the large (0·42, v'nce 0·085) : in the other case the increase was similar with both nest pans (0·27).

In a number of cases where the data round the start of egg laying were complete, straight lines of $\xi = \alpha + \beta x$, where $\xi = \log_e \frac{r+\frac{1}{2}}{n-r+\frac{1}{2}}$ and $x =$ date in relation to egg laying, were fitted to the data. The results are shown in Table 22. (See also Fig. 9). It will be seen that :

(a) The gradient of the lines was always positive, showing that changes in internal factors lead to an increase in the proportion of feathers as the cycle progresses.

(b) The proportion of feathers was usually greater than 50 per cent on Day 0 (i.e. Intercept > 0) with Pan A, and invariably so with the substituted pans.

TABLE 22

Change in proportion of feathers brought to nest in relation to date of first egg and type of nest pan. Characteristics of straight line $\xi = \alpha + \beta x$ where x = day in relation to laying of first egg, $\xi = \log \frac{r+\frac{1}{2}}{n-r+\frac{1}{2}}$, n = total number of placings in 30-min. watch, r = no. of placings of feathers in watch.

Nature of pan	Pan B		Pan A		Difference B–A	
	Intercept α	Gradient β	Intercept α	Gradient β	t α	t β
Small hard substituted 24 hrs. earlier	0·415 ±0·179	0·013 ±0·060	−0·136 ±0·190	0·138 ±0·051	(+) 2·1	(−) 1·6
	1·908 ±0·717	0·193 ±0·108	1·099 ±0·404	0·288 ±0·080	(+) 1·0	(−) 0·7
	0·894 ±0·268	0·048 ±0·039	0·049 ±0·173	0·140 ±0·030	(+) 2·6	(−) 2·2
	0·583 ±0·210	0·403 ±0·100	0·544 ±0·221	0·214 ±0·085	(+) 0·1	(+) 1·4
	0·606 ±0·313	0·351 ±0·132	−0·590 ±0·305	0·358 ±0·114	(+) 2·7	(−) 0
Small grass substituted 24 hrs. earlier	3·463 ±0·782	0·279 ±0·081	1·750 ±0·404	0·299 ±0·045	(+) 1·9	(−) 0·2
	1·968 ±0·405	0·681 ±0·131	2·792 ±0·563	0·673 ±0·220	(−) 1·2	(+) 0
	2·478 ±0·395	0·483 ±0·063	2·323 ±0·455	0·280 ±0·066	(+) 0·3	(+) 2·2
Small hard substituted just before	1·068 ±0·319	0·483 ±0·113	0·466 ±0·281	0·441 ±0·108	(+) 1·4	(+) 0·3
	0·779 ±0·192	0·110 ±0·073	0·134 ±0·208	0·216 ±0·024	(+) 2·3	(−) 1·4

(c) The proportion of feathers on Day 0 was (with one exception) always greater with the substituted pan (i.e. intercept with Pan B> than that with Pan A). In four cases the difference was significant.

(d) The gradient of the lines derived from the data with Pan B was less than those derived from the Pan A data in six out of ten cases : this was significant in only one case and in one case it was significant in the opposite direction. Thus no generalisation as to the relative effectiveness of Pan A as the nesting cycle advances can be made.

(d) *Conclusions*

The selection of nest material is thus governed by both internal and external factors. Among the latter the size and texture of the nest-cup are important.

It is noteworthy that, in the preliminary incomplete nesting cycles shown in Fig. 2, the proportion of feathers does not run parallel to the weight of material brought to the nest, even though the external situation at the beginning of each day is constant. These two factors must therefore depend on different aspects of the internal state.

10. BIZARRE BUILDING HABITS

In this section a number of abnormal types of building behaviour are discussed. These appeared in birds which were or had been deprived of nest material, and throw some light on the learning processes which normally integrate the component patterns of nest-building into a functional whole.

All the birds discussed here were in their first year. The following types of deprivation were employed :

(a) Total deprivation. The birds were kept without any nest-material or similar substance either from an age of c. ten days or at least during the ten weeks preceding the onset of building in their first spring. In practice it was not possible to be absolutely certain that they *never* had material of any sort, for their own bodies were a source of feathers.

(b) Partial deprivation. Material was present for the duration of the half hour daily watch only, as described in Section 7.

The principal types of abnormal behaviour were :

(a) Plucking own breast feathers. Some females pulled out their own breast feathers. In some cases this led to quite large areas of the breast being denuded. One female frequently attempted to pluck her mate's feathers.

Similar behaviour was seen in some female hand-reared Chaffinches (*Fringilla coelebs*) which were kept, for the purpose of another experiment, in an indoor flight throughout their first breeding season. Two of these birds were given opportunity to breed in an outdoor aviary with plenty of material in two subsequent summers, but each time they plucked their own breasts bare just as they had done the first year.

(b) Carrying own feathers but not plucking. Some canaries, instead of actually plucking their own feathers, would pick one up without detaching it from the skin, fly to the nest-pan holding on to it, settle down in the pan and go through the motions of placing it and building. Any one individual would usually pick up a feather from the same body region on every occasion : when the feather was attached to the back or lower breast, this could involve flying to the nest in a very contorted position. The behaviour was usually stereotyped—some females would always go to the same point in the cage in order to pick up their own feathers.

(c) Carrying from nest-pan. If a female deprived of material managed to obtain one small particle of it (e.g. by pulling out one of her own feathers), she might then show building behaviour normal in every way except that this same piece of material would be used in every bout. Each sequence of

nest-building behaviour would start with the collection of the feather from the nest-pan : the feather was then carried backwards and forwards a few times, replaced in the pan, and " built in ".

Even when material was present, previously deprived females would sometimes carry material away from the pan after a spell of sitting (building). The proportion of sitting bouts followed by carrying in this way showed only a slight decrease with increasing frequency of bouts, and so this behaviour is not to be understood in terms of an exceptionally low or high level of motivation.

(d) Wall-writing etc. One female persistently " wrote " with wide sweeps of her beak on the enamelled wall of the cage. This occurred in two successive seasons. The behaviour was especially common when she was deprived of material, persisted when material was provided, but then occurred only when she was carrying material. It was therefore probably connected with nest-building, but its origin and significance are unknown. Another female spent much of her time pecking at the enamel of the cage walls and others frequently pulled at the wire netting cage front as though trying to detach it.

(e) Gathering through bottom of nest pan. Most of the nest-pans used in these experiments had small ventilation holes in the bottom. Some females would frequently gather, through these holes, the material which they had just placed in the nest-pan. This occurred also in non-deprived birds.

The incidence of some of these habits is shown in Table 23 a–d. The following conclusions can be drawn :

(a) Plucking and/or carrying of the female's own feathers was never seen in undeprived birds when material was present (Table 23a) nor did it appear in two birds which were subjected to total deprivation after completing their first cycle normally (Table 23 b). It was, however, observed in four out of five birds which were totally deprived during their first cycle (Table 23 c) and in five out of seven which were partially deprived (Table 23 a). When these birds were given material, however, the habit disappeared immediately in nearly every case.

(b) Carrying of material away from the nest was never seen in six out of ten undeprived birds, and was rare in three others (Table 23 a). The exceptional behaviour of the tenth bird is discussed below. Two of these birds which were subjected to deprivation after their first cycle (Table 23 b) subsequently carried material from the nest, one of them much more often than before.

Carrying from the nest occurred when all totally deprived birds were subsequently given material. In all four cases it was more marked during the period of partial deprivation than in the later period when material was continuously present (Table 23 c).

Carrying from the nest also occurred in all partially deprived birds—in fact it was even more frequent here than in totally deprived ones. Of four such birds which were subsequently watched with material continuously present, two carried from the nest much less frequently than, and two about as often as before (Table 23 a and d). There was no consistent difference between the behaviour immediately after material was supplied and the behaviour ten days afterwards.

It is thus clear that these abnormal building habits are associated with the deprivation of material. The carrying of material away from the nest is probably the result of learning during deprivation, when the female built repeatedly with a single piece of material. If the female cannot build normally, she develops habits which allow at least some of the building behaviour to be shown. The performance of some parts of nest-building behaviour thus has a reinforcing value even if no nest is built—just as eating without ingestion or intromission without ejaculation has reinforcing value for some mammals. When abundant material is supplied to previously deprived birds, the greater persistence of carrying from the nest than of carrying or plucking own feathers

TABLE 23

Incidence of abnormal building habits. (a) First cycles.

Degree of deprivation	Pair No.	Deprived of material			Material present				
		No. of 15-min. watches	No. of watches in which gathered own feathers	Time spent gathering own feathers	No. of 30-min. watches	No. of watches gathered own feathers	Time spent gathering or carrying own feathers	No. of placings observed	No. of times carried material from nest as % of no. of placings
Material always present	19/56				30	0	0	263	0·4
	33/56				10	0	0	79	0
	54/56				16	0	0	99	0
	41/56				9	0	0	37	0
	11/56				11	0	0	63	5
	12/56				11	0	0	48	0
	20/56				5	0	0	10	0
	4/57				9	0	0	78	3
	12/57				4	0	0	24	0
	3/57				27	0	0	209	40
A little material always plentiful only during watch	10/57				27	0	0	284	11·0
	11/57				11	0	0	165	11·5
	17/57				20	0	0	177	2·9
	27/57				23	0	0	363	21·2
	29/57				28	0	0	397	42·1
	35/57				23	0	0	413	15·5
Material during watch only	2/56	11	1	174	15	0	0	261	6·1
	26/56	5	4	1051	15	0	0	321	2·8
	1/56	12	0	0	13	0	0	409	6·3
	18/56	7	0	0	10	0	0	90	2·4
	9/56	10	1	11	15	0	0	281	16·7
	25/56	2	1	58	3	1	113	25	8
	27/56	3	1	39	6	2	56	34	30
	12/56	0	—	—	5	0	0	206	2·4
	30/57	0	—	—	18	0	0	196	18

(b) Undeprived first cycle. Total deprivation second cycle to first egg or for 30 days, then partial deprivation for 2 to 3 days, then material continuously present.

Pair No.	No material present			Material present for watch only					Material continuously present				
	No. watches (15 mins.)	No. watches in which carried own feathers	Mean time (secs.) carrying own feathers	No. watches	No. watches carried own feathers	Time (secs.) carrying own feathers	No. placings observed	No. carried from nest as % of placings	No. watches	No. watches carried own feathers	Time (secs.) carrying own feathers	No. placings observed	No. carried from nest as % of placings
12/57	3	0	0	1	0	0	17	23	6	0	0	63	13
4/57	6	0	0	3	0	0	29	3	3	0	0	27	3

(c) Total deprivation to first egg or for 30 days. Then watches with no material, and with partial deprivation for 2 to 3 days, then material continuously present.

1/57	4	1	142	3	0	0	72	18	10	0	0	169	7·9 (nearly all in 1st 4 days)
9/57	3	2	467	1	0	0	25	72	3	0	0	26	8
2/57	5	0	0	1	0	0	12	25	4	0	0	42	2
19/57	5	4	Fre-quent	4	0	0	36	36	2	0	0	15	28
15/55	9	4	do.	6	3	Occa-sional	No. record						

(d) Subsequent behaviour of birds partially deprived first cycle.

Pair No.	1st 10 days after end of deprivation			More than 10 days after end of deprivation		
	No. watches	No. placings observed	Carried from nest as % of placings	No. watches	No. placings observed	Carried from nest as % of placings
10/57	3	39	15	2	34	12
11/57	12	52	10	3	10	20
27/57	4	76	12	1	36	0
29/57	4	23	20	2	22	23

must be related to the physical difficulty of the latter. It is as easy to gather from the pan as from the floor, and this habit shows little extinction.

It is also clear that if there is no deprivation these habits are not learnt, but rather the bird builds (or learns to build) constructively. That the female does not pluck or carry her own feathers under normal conditions is not surprising. That she does not carry material away from the nest must be related to learning during site selection.

The change-over from performing building movements without material to building with material, which occurs in normal cycles (p. 5), depends on the internal state. The one bird which was not deprived, but did carry material from the nest, did not come into full condition in the normal fashion, but first built in a dilatory fashion for over five weeks. During this period, sitting (building) was relatively infrequent. It could be, therefore, that there is a reinforcing value of building constructively which is less important when motivation is low (see below). It is still not clear, however, why carrying material from the nest does not drop out of the behaviour of deprived birds more rapidly when material is plentiful.

Thorpe (1956) has suggested that the building of a species-characteristic nest has greater reinforcing value than building in any other way—he thus postulates a reinforcing value of the result of building as well as in the performance of building behaviour. This study has shown that stimuli from the near-completed nest produce a decrement in building behaviour, which is a necessary corollary of Thorpe's hypothesis, but otherwise neither confirm nor deny it. It must be remembered, however, that these canaries were building under artificial and simplied conditions, with a nest-pan already provided in which they could shape the nest : data more relevant to Thorpe's thesis could be obtained under more natural conditions.

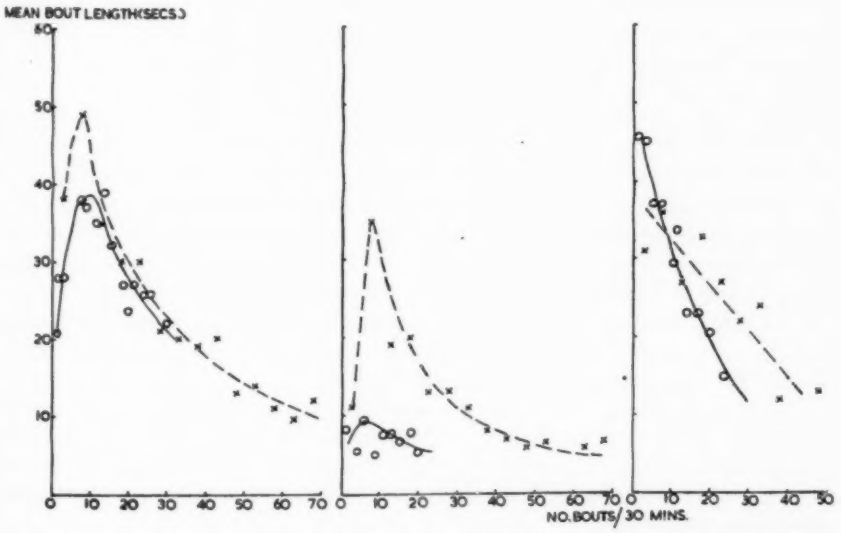


Fig. 10.—Relation between mean bout lengths of (left to right) gathering, carrying and sitting, and the number of bouts of each activity per watch. Crosses and discontinuous lines refer to deprived birds, circles and continuous lines to birds with material continuously.

One further point may be mentioned here. Fig. 3 shows that, for a given total time building, the total times spent gathering and carrying is slightly greater, and the total time spent sitting is less, with birds which have been partially deprived of material than with those birds which have had material continuously. This effect of deprivation is even more clear when bout lengths are plotted. Fig. 10 shows the relation between the mean bout length of each activity against the number of bouts of that activity in the watch. The gathering and carrying bouts of deprived birds are consistently longer than those of undeprived birds, the effect being most marked with carrying.

11. THE BUILDING BEHAVIOUR OF NAIVE BIRDS

Under natural conditions nest construction involves the functional integration of a number of responses. This integration clearly involves learning at every stage—e.g. learning the individual characteristics of the chosen nest-site, learning sources of nest material, the route to the nest-site, and so on. In terms of reinforcement theory, we have seen that some of the habits formed imply a reinforcing value in the mere performance of building behaviour, others perhaps in the actual construction of a nest.* In view of this, it is worth while listing those aspects of building behaviour which appear in naive females, and in birds which were removed from their parents' nest, placed in a bare nest-pan before they could fly, and allowed no access to nest material until their first breeding season. (Of course it was impossible to deny these birds access to their own feathers, but loose feathers were removed from the bottom of the cage as soon as they were seen).

(a) The nest-pans were chosen as nest-sites in preference to the corners of the cage, etc., by females removed from their parents when a few days old, just as by birds reared normally. One female who was kept also without a nest-pan, laid her eggs in the seed dish, which in shape resembled the nest-pan. Another female, who was given a nest-pan for the first time twelve days before she laid her first egg, inspected it frequently during the following minutes and brought material for the first time after twenty-seven and a half minutes : the male was rather faster, bringing material to the nest-pan for the first time after twenty minutes.

(b) Females in breeding condition who had never had nest-material would go through all the movements of building in the nest-pan—scrabbling, pulling in, wiping and so on. They would also hop over the floor of the cage going through the movements of searching for material.

(c) When material was presented for the first time, the response of those females in breeding condition was rapid and appropriate. In Table 24 are shown the delays between the first presentation of material and the onset of gathering, carrying and placing, each watch being continued for thirty minutes. Although the date with reference to laying of the first egg is no guide to condition for dates more than ten days before the egg date (see p. 10), all the birds who were definitely nearing the point of lay responded to the material almost immediately.

* Verlaine (1934) and Promptov (1956) report improvement in nest-building ability with practice, but their observations are difficult to assess. There is great individual variation in tidiness amongst the nests of both naive and practised birds.

TABLE 24

Latency of building responses after first presentation of material to naive females. * indicates a female reared from c. eight days without access to building material : the others were without material for a few months before nesting.

Cage No.	Day	Latency (secs.) to beginning of first		
		Gathering	Carrying	Placing
9/57	0	4	72	130
36/57	–5	8	68	176
*2/56	–6	18	68	110
1/57	–7	2	48	148
9/56	–8	4	21	255
35/57	–9	50	91	140
*1/56	–11	7	22	62
33/56	–12	120	1080	—
17/57	–15	54	92	157
26/56	–17	5	67	95
*4/55	–18	4	24	60
11/56	–18	60	—	—
25/56	–22	24	840	840
	–28	27	67	300
34/56	–28	6	390	—
41/56	–29	1050	—	—
19/56	–35	90	100	—

(d) The change-over from the bringing of grass to the bringing of feathers occurred in naive birds whose nests were removed daily just as with experienced birds (see, e.g. Fig. 2).

(e) Naive females whose nests were removed daily brought more material in total than at later nests where they were undisturbed. (The females cited on p. 31 were in fact naive).

(f) To a superficial inspection, nests built by deprived and naive birds were as large and tidy as those built by experienced ones.

It is thus clear that the movements of nest-building and the responses to material are independent of previous experience of material. Further these responses, together with at least most of the other responses to stimuli (releasing and consummatory) involved in nest-building, are independent of any previous experience of a perfect nest.

12. CONCLUSION

Nest-building employs relatively few movements, yet leads to the construction of a nest which, in some species, may be very complicated and finely built. Thorpe (1956) has suggested, and this study confirms, that nest-construction depends not merely on a number of species-characteristic motor patterns, but on their integration through appropriate responsiveness to stimulus situations which either release, inhibit or reinforce behaviour. Thus the releasing effect of the nest-pan and material, and the various effects of stimuli from the half-completed nest on the selection of material, on the nature of the building

behaviour, and on the ultimate inhibition of that behaviour, play an essential role in the integration of building. Many of these stimulus situations are effective although the bird has had little experience of them—indeed the way in which stimuli from the half-completed nest influence the intensity of building and the selection of material show that the bird responds to stimuli characteristic of a nest which it has not yet built. The building of the nest thus depends both on stereotyped motor patterns, and on responsiveness to stimuli, which appear in naive birds. The behaviour of birds deprived of material shows that the integration of the constituent patterns depends on learning—the performance of one activity bringing the animal into a situation where it can perform the next, and so being reinforced. As with hoarding in rats (Marx, 1950) and the parental behaviour of ring doves (*Streptopelia risoria*) (Lehrman, 1956), nest-building thus involves an integration of different components with learning playing an important role. The ontogeny of nest-building, like the parental behaviour of other species (Lehrman, 1956), is, however, complex, and this paper represents only the first stage in its analysis.

SUMMARY

1. The nest-building behaviour of domesticated canaries was studied.

2. The principal activities, or groups of activities, studied were inspecting, gathering, carrying and sitting (building). The latter includes a number of stereotyped motor patterns functioning in shaping the cup.

3. The nest-site is selected by the female as or before building begins.

4. Building activity reaches its peak three or four days before the laying of the first egg, and slightly before the peak of copulation. The temporal relations between building and egg-laying are highly variable between individuals. The male plays only a small part in nest-building.

5. The total times spent gathering, carrying and sitting per watch are positively correlated. Since the change-over from one activity to the next does not depend solely on external stimuli, this suggests that these activities share internal causal factors.

Two characteristics of building behaviour (total time building per watch and number of placings per watch) are not fully correlated with each other, and there are differences between the relations of the total times spent gathering, carrying and sitting with each of these characteristics (Figs. 3 and 4). The concept of a nest-building drive is thus not useful, for the selection of criteria whereby it could be quantified is arbitrary.

The median bout lengths of gathering, carrying and sitting first increase and then decrease with increase in the number of placings per watch (Figs. 5 and 6) and there are correlations between the bout lengths of the different activities in each nest-building sequence. Each activity can be interrupted by the activity which functionally follows it before it own motivation has fallen to the normal threshold.

The appetitive/consummatory behaviour dichotomy is not useful in analysing the relationships between gathering, carrying and sitting, but these can be understood in terms of concepts such as common causal factors, threshold differences, and self-suppressing effects consequent upon performance.

6. The stereotyped movements of nest-building differ in frequency between individuals. " Scrabbling " is influenced by the size of the nest.

7. The decrease in nest-building activity around the time of egg-laying is due partially to internal changes, and partially to stimuli from the nest.

8. The length of sitting bouts is influenced by stimuli from the nest-pan as well as internal factors.

9. The change-over from building with grass to building with feathers which occurs shortly before egg-laying is due partially to internal changes and partially to stimuli from the nest.

10. Canaries reared without material show a number of bizarre patterns of behaviour which are established by learning during deprivation. The mere performance of nest-building movements has some reinforcing value.

11. Many of the constituent patterns of nest-building behaviour occur in naive birds, but their integration is partially dependent on learning.

ACKNOWLEDGMENTS

I am very grateful to Dr W. H. Thorpe and Dr J. J. A. van Iersel for reading the manuscript, and making many helpful comments and suggestions. The work was facilitated by a grant from the Royal Society for the purchase of a Gregory-Russell recorder. I am also very indebted to Professor H. E. Daniels for guidance and help with the statistical treatments used in Section 9.

REFERENCES

Anscombe, F. S. (1956). On estimating binomial relations. *Biometrika* **43,** 461.

Armstrong, E. A. (1955). *The wren.* London.

Bastock, M. & Manning, A. (1955). The courtship of *Drosophila melanogaster*. *Behaviour* **8,** 85.

Craig, W. (1918). Appetites and aversions as constituents of instincts. *Bull. Biol.* **34,** 91.

Deckert, G. (1955). Beiträge zur Kenntnis der Nestbau-Technik deutscher Sylviiden. *J. Orn.* **96,** 186.

Dobben, W. H. van (1949). Nest building technique of icterine warbler and chaffinch. *Ardea* **37,** 89.

Dunnett, G. E. & Hinde, R. A. (1958). Chapter on passerines in *U.F.A.W. Handbook on care and management of laboratory animals.* Ed. by A. N. Worden and W. Lane-Petter. London.

Fisher, R. A. & Yates, F. (1938). *Statistical tables for biological, medical and agricultural research.* London.

Gregory, R. L. (in press). Electromagnetic digital printing recorder. *J. Sci. Instr.*

Hinde, R. A. (1952). The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour* Suppl. No. 2.

Hinde, R. A. (1955). A comparative study of the courtship of certain finches. *Ibis* **97,** 106; **98,** 1.

Hull, C. L. (1943). *Principles of behaviour.* New York.

Howard, H. E. (1929). *An introduction to the study of bird behaviour.* Cambridge.

Iersel, J. J. A. van (1953). An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus*). *Behaviour* Suppl. No. 3.

James, William (1892). *Text book of psychology.* London and New York.

Kramer, G. (1950). Der Nestbau beim Neuntöter (*Lanius collurio* L.). *Ornith. Ber.* **3,** 1.

Lehrman, D. S. (1956). On the organization of maternal behaviour and the problem of instinct. In *L'instinct dans le comportement des animaux et de l'homme.* 475. Paris: Fondation Singer-Polignac.

MARLER, P. (1957). The behaviour of the chaffinch. *Behaviour* Suppl. No. 5.
MARX, M. H. (1950). A stimulus response analysis of the hoarding habit in the rat. *Psychol. Rev.* **57**, 80.
PROMPTOV, A. N. (1956). *Essays on the problem of the biological adaptiveness of the behaviour of passerine birds.* Moscow: Acad. Sci. U.S.S.R.
RUSSELL, W. M. S., MEAD, A. P. & HAYES, J. S. (1954). A basis for the quantitative study of the structure of behaviour. *Behaviour* **6**, 153.
SHERRINGTON, C. S. (1906). *The integrative action of the nervous system.* New York.
THORPE, W. H. (1956). *Learning and instinct in animals.* London.
VERLAINE, L. (1934). L'instinct et l'intelligence chez les oiseaux. *Recherches Philos.* **3**, 285.

DACTYLOPUSIOIDES MACROLABRIS (CLAUS) (COPEPODA: HACPACTICOIDA) AND ITS FROND MINING NAUPLIUS

BY

J. GREEN

Bedford College, University of London

[Accepted 12th November 1957]

(With 13 figures in the text)

CONTENTS

	Page
Introduction	49
Description of the nauplius	49
Description of the adult	51
Discussion	51
Acknowledgments	53
Summary	53
References	53

INTRODUCTION

During an examination of some fronds of the brown seaweed *Dictyota dichotoma* Lamour, collected from Torquay in July 1957, several harpacticoid nauplii were found in small galleries, or mines, between the two epidermal layers of the alga. The purpose of this paper is to describe these nauplii and to determine their systematic position.

DESCRIPTION OF THE NAUPLIUS

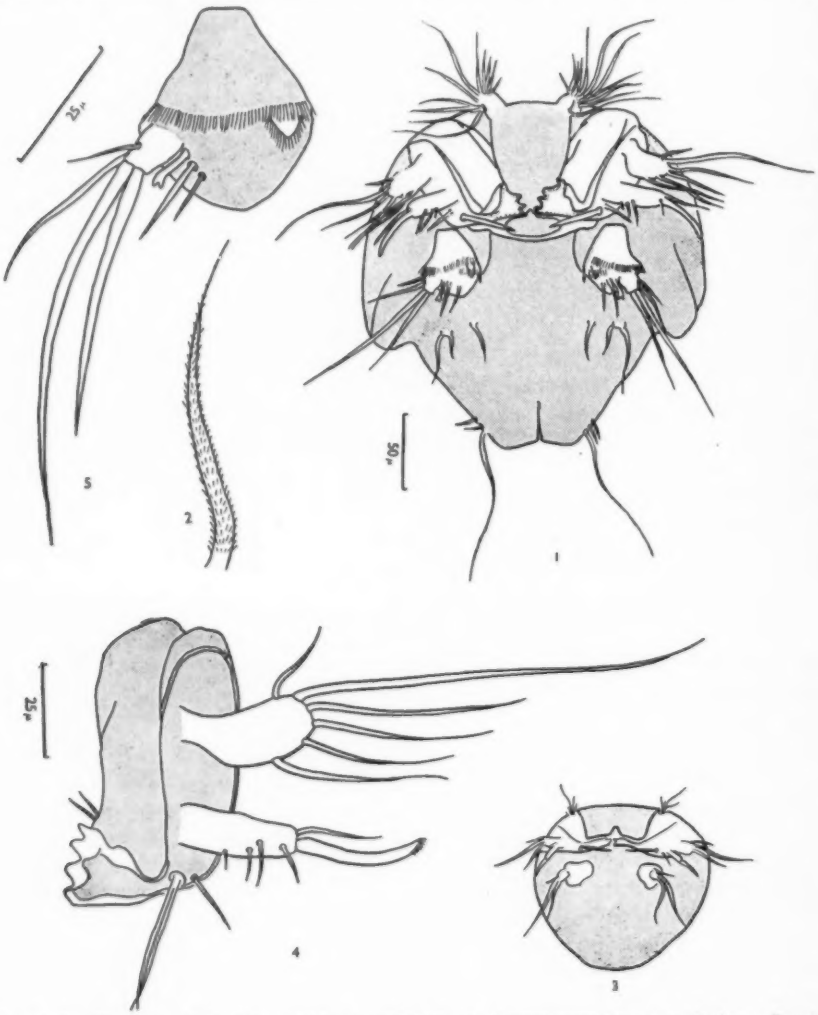
The nauplii vary in length from 103 to 234μ. The description which follows applies to the largest nauplius; the smaller nauplii were similar in structure, but had fewer setae on the appendages and body. Several specimens were mounted in polyvinyl-lactophenol and stained with lignin pink or chlorazol black.

The body of the nauplius is rounded, with the posterior part narrowed. In the largest specimen the narrower hindpart is clearly demarcated (Fig. 1), but in the smaller specimens the body is more evenly rounded.

The first antenna is a simple projection with a number of fine setae, some of which, when viewed under an oil immersion objective, have very fine processes projecting from all over their surfaces (Fig. 2). The second antennae are modified to form biting appendages; they have strong biting gnathobases. A large seta projects from each gnathobase towards the mouth. At first sight this seta appears to be blade like, but in fact it has two branches which lie side by side, or it might even be two setae lying side by side. However, there appears to be a common pit at the insertion, and I cannot separate two setae at the base. There are two small setae on the medial border, just inside the biting part. The endopod and exopod are each formed from a single podomere.

The exopod has six setae, while the endopod also has six, but more variable in size. One of the terminal setae on the endopod is large, and has fine unilateral feathering at its tip.

The third appendage, which must be the morphological equivalent of the adult mandible, consists of two podomeres. There is a large basal podomere, with a curious triangular flap near its medial border, and a ring of microtrichs, and a smaller, distal podomere bearing four setae, two of which are very



Figs. 1–5.—Nauplius of *Dactylopusioides macrolabris*. 1, largest nauplius, ventral view. 2, one seta from the first antenna, greatly enlarged. 3, smallest nauplius, drawn to the same scale as Fig. 1. 4, second antenna, ventral view. 5, third appendage, or mandible, ventral view.

large. Alongside the distal podomere, on the basal podomere, are three setae, one of which has a forked end.

Three setae are found on the body just behind the mandible ; these probably represent the maxillule. A further three setae are found in the position of future furcal setae.

DESCRIPTION OF THE ADULT

A single copepodid and a single adult female were found inhabiting mines on the same frond as the nauplii. They were both of the same brilliant crimson colour as the nauplii.

Using the key in Lang's monograph (1948) the adult female was identified as *Dactylopusioides macrolabris* (Claus). The original description by Claus (1866) and the description of *D. stampaliae* by Brian (1928) have also been examined. This has confirmed Lang's view that *D. macrolabris* and *D. stampaliae* are synonymous. In order to establish the validity of the identification of the single female as *D. macrolabris* most of the important taxonomic features are illustrated in Figs. 6–13. These figures also shows some features which have not previously been adequately illustrated. Figure 6 shows that some of the setae on the second podomere of the first antenna are stouter editions of those on the first antenna of the nauplius. This strengthens the view that the female really is the adult of the nauplius. The only really conclusive way of establishing this would be to find a female with fully developed nauplii in its egg sac, as Harding (1954) did with *Thalestris rhodymeniae*.

The distal podomere of the exopod of leg 2 had two setae on its inner border (Fig. 10), a point which agrees with Lang's view that Monard's (1935) figure showing three setae in this position is incorrect.

Monard's figure of the first leg shows a strong straight seta on the inner border of the second podomere of the exopod. This is very difficult to see in the specimen from Torquay, in which it is weak, curved and transparent.

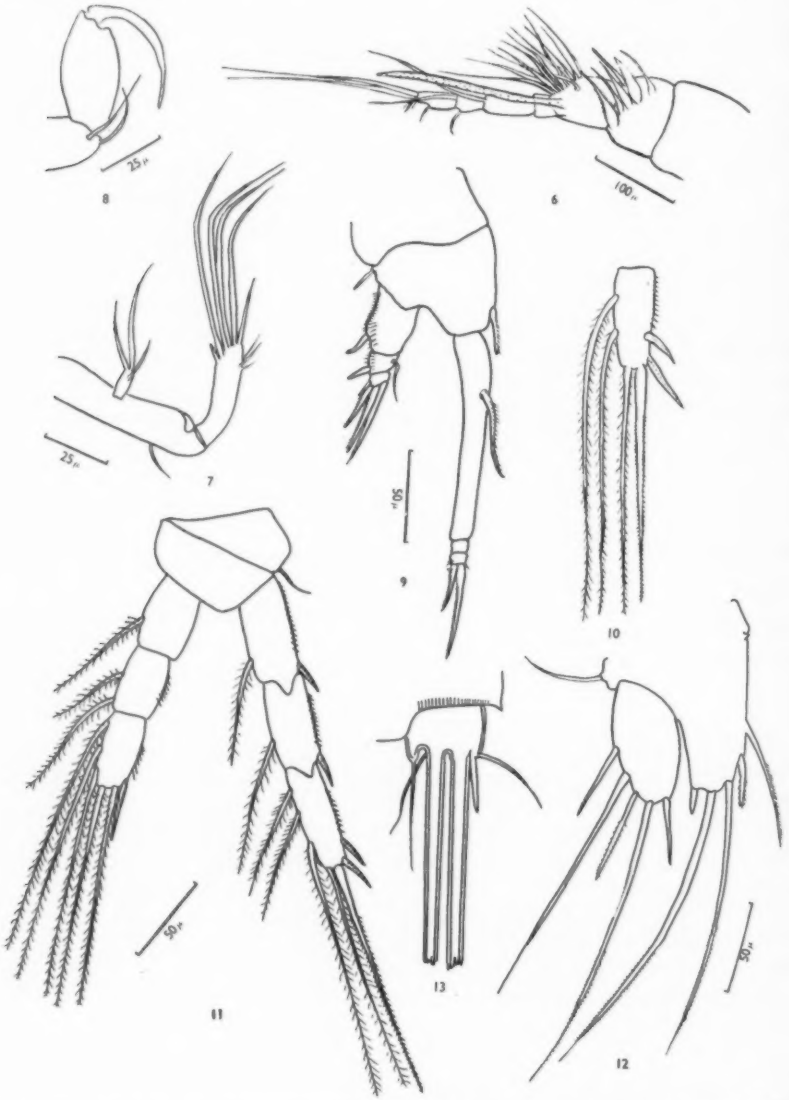
DISCUSSION

The habit of burrowing between the epidermal layers of an alga, as done by the nauplii of *Dactylopusioides*, is reminiscent of the habits of various larval insects which burrow in a similar manner in the leaves of phanerogamous plants. These insects are known as leaf miners (see Hering, 1951, for a general account). The term frond miner seems a reasonable parallel to apply to the nauplii described above.

The present record of *Dactylopusioides macrolabris* appears to be the first for Britain, and is the first record of a miner in the fronds of a phaeophycean alga. Three other species of harpacticoid copepods are known to have similar habits, but mining in Rhodophyceae instead of Phaeophyceae.

Bocquet (1953) described *Diarthrodes feldmanni*, which is found in the fronds of several species of Rhodophyceae. All stages of this copepod, from the first nauplius to the fifth copepodid are found in galleries in the thallus of the alga. The copepod eats the interior of the thallus, leaving only the cuticle. The early stages form a linear gallery, but the later stages widen out a terminal chamber.

Fahrenbach (1954) described *Diarthrodes cystoecus*, the adults of which live in the water-filled, bladder-like thalli of the red alga *Halosaccion glandiforme*. The nauplii burrow into the wall of the bladder, and produce small cysts which project above the outer surface of the algal thallus. The copepod



Figs. 6–13.—Adult female of *Dactylopusioides macrolabris*. 6, first antenna. 7, second antenna. 8, maxilliped. 9, first leg. 10, third podomere of the exopod of the second leg. 11, third leg. 12, fifth leg. 13, caudal ramus ; the two long setae are shown as broken off.

becomes mature within the cyst, and escapes to the inside of the bladder through a small hole.

Both Bocquet and Fahrenbach state that they found the nauplii of their respective species, but they did not describe them.

Harding (1954) redescribed the nauplius originally described by Brady (1894) as *Fucitrogus rhodymeniae*, and described the adult, showing it to be a member of the genus *Thalestris*, Harding's description of the nauplius clarified the homologies of the appendages, and shows marked similarities to the nauplius described in the present paper, particularly in the presence of a powerful biting gnathobase on the second antenna. The first antenna of the nauplius of *T. rhodymeniae* bears peculiar fir cone-like processes (presumably modified setae) ; these are absent from the nauplius of *Dactylopusioides*, but certain of the setae show a slight tendency in this direction in their structure (Fig. 2).

The genera *Thalestris*, *Diarthrodes* and *Dactylopusioides* all belong to the family Thalestridae, many members of which are recorded in Lang's monograph as living among algae. It seems probable that other members of this family will be found to have frond mining habits, and it will be of great interest to see if all the species have the second antennae of their nauplii as strongly modified as the second antennae of *Thalestris rhodymeniae* and *Dactylopusioides macrolabris*.

ACKNOWLEDGMENTS

The specimens described above were collected while working at the Plymouth Marine Laboratory ; my thanks are due to the Director and staff for the facilities which they provided. Dr Mary Park kindly identified *Dictyota* for me. I am most grateful to Dr J. P. Harding for some helpful discussion and for reading the manuscript.

SUMMARY

The nauplius of *Dactylopusioides macrolabris* (Claus) is described and figured. The second antenna is modified to form a biting appendage, while the mandibles are not capable of biting.

The nauplii and an associated adult female were found in galleries in the fronds of the brown alga *Dictyota dichotoma*, from Torquay, Devon. This is the first British record of this copepod, and the first record of a copepod mining the fronds of a member of the Phaeophyceae.

REFERENCES

Brady, G. S. (1894). *On Fucitrogus Rhodymeniae*, a gall-producing copepod. *J. R. micr. Soc.* **1894,** 168–170.

Brian, A. (1928). I Copepodi Bentonici marini. *Arch. zool. (Ital.) Napoli* **12,** 293–343.

Bocquet, C. (1953). Sur un Copépode Harpacticoide mineur, *Diarthrodes feldmanni* n. sp. *Bull. Soc. zool. Fr.* **78,** 101–105.

Claus, C. (1866). Die Copepodenfauna von Nizza. *Schr. Ges. ges. Naturw. Marburg.* **9,** suppl. 1, 1–34.

Fahrenbach, W. (1954). A new species of the genus *Diarthrodes* (Crustacea, Copepoda) parasitic in a red alga. *J. Wash. Acad. Sci.* **44,** 326–329.

HARDING, J. P. (1954). The copepod *Thalestris rhodymeniae* (Brady) and its nauplius, parasitic in the seaweed *Rhodymenia palmata* (L.) Grev. *Proc. zool. Soc. Lond.* **124,** 153–161.

HERING, E. M. (1951). *The biology of leaf miners.* The Hague.

LANG, K. (1948). *Monographie der Harpacticiden.* **1** & **2.** Lund.

MONARD, A. (1935). Les harpacticoides marins de la région de Salammbô. *Bull. Stat. oceanogr. Salammbô.* No. 34, 1–94.

THE ANATOMY AND PHYSIOLOGY OF THE REPRODUCTIVE SYSTEM OF THE FRESHWATER SNAIL *PHYSA FONTINALIS* (L.)

BY

C. J. DUNCAN

*Department of Zoology, Queen Mary College, University of London**

[Accepted 12th November 1957]

(With 13 figures in the text)

CONTENTS

	Page
Introduction	55
Material and methods	57
Ovotestis	58
Hermaphrodite duct	59
Albumen gland	61
The male system	
The vas deferens	65
The prostate	66
Vas deferens (distal region)	67
The penial complex	67
The female duct	
Oviduct	70
Vagina	72
The bursa copulatrix	73
Fertilisation	76
Secretion by the albumen gland	76
Formation of the egg capsule	77
Discussion	79
Acknowledgment	81
Summary	81
References	82

INTRODUCTION

The annual cycle, copulation and oviposition of the freshwater snail *Physa fontinalis* (L.) have been described previously (Duncan, 1958) and in the present paper the structure and function of the reproductive system of this species are considered. The relationships between the Physidae and other families of the Pulmonata, as shown by the genital systems, will be discussed in a subsequent publication. The Physidae is one of the four higher limnic families of the Basommatophora which together constitute the group Hygrophila.

A number of anatomical descriptions of the genital systems of members of the Hygrophila have been published. In 1869, Eisig produced an account of the anatomy of *Lymnaea auricularia*, while six years earlier, Baudelot (1863) included morphological descriptions and figures of the genital systems of

* Present address : Department of Zoology, The University, Liverpool.

Edwards, J. P. (1956). The copepod *Thalestris rhodymeniae* (Brady) and its nauplius, parasitic in the seaweed *Rhodymenia palmata* (L.) Grev. *Proc. zool. Soc. Lond.* **124,** 153–161.

Hering, E. M. (1951). *The biology of leaf miners.* The Hague.

Lang, K. (1948). *Monographie der Harpacticiden.* **1** & **2.** Lund.

Menard, A. (1925). Les harpacticoïdes marins de la région de Salammbô. *Bull. Stat. oceanogr. Salammbô.* No. 34, 1–94.

THE ANATOMY AND PHYSIOLOGY OF THE REPRODUCTIVE SYSTEM OF THE FRESHWATER SNAIL *PHYSA FONTINALIS* L.

BY

C. J. BETTIS

*Department of Zoology, Queen Mary College, University of London.**

(Communicated by [illegible])

(With [illegible] figures in the text)

CONTENTS

Page

[illegible] 1
[illegible] 2
[illegible] 3
[illegible] 3
[illegible] 4
The [illegible]
The [illegible] 6
The [illegible] 9
The [illegible] [illegible] 11
The [illegible] 11
The [illegible]
[illegible] 13
[illegible] 13
The [illegible] 15
[illegible] 15
[illegible] [illegible] 17
[illegible] [illegible] 18
[illegible] 19
[illegible] 21
[illegible] 21
[illegible] 22

INTRODUCTION

The anatomy, life, reproduction and classification of the freshwater snail *Physa fontinalis* L. have been described previously (Bettis, 1954) and in the present paper the structure and function of the reproductive system of this species are considered. The relationship between the Prostate and other organs of the Pulmonata, as shown by the genital system, will be discussed in a subsequent publication. The Prostate is one of the most highly developed organs of the Gastropoda, which together constitute the group Streptoneura.

A number of anatomical descriptions of the genital system of members of the Basommatophora have been published. In 1849 Lang published an account of the anatomy of *Lymnaea peregra*, which was soon rather thoroughly [illegible] anatomical descriptions and figures of the genital system of

* Present address: Department of Zoology, The University, Liverpool.

L. stagnalis and *Planorbarius corneus*. Other studies include those of Lacaze-Duthiers (1899), Baker (1928), Germain (1930) and Hoff (1940), although in general these describe the gross morphology only. The first histological account was produced by Slugocka (1913), who studied members of the Physidae, and this has been followed by the description of the reproductive system of *L. stagnalis* by Holm (1946) and two members of the Planorbidae (Abdel-Malek, 1954 a and b).

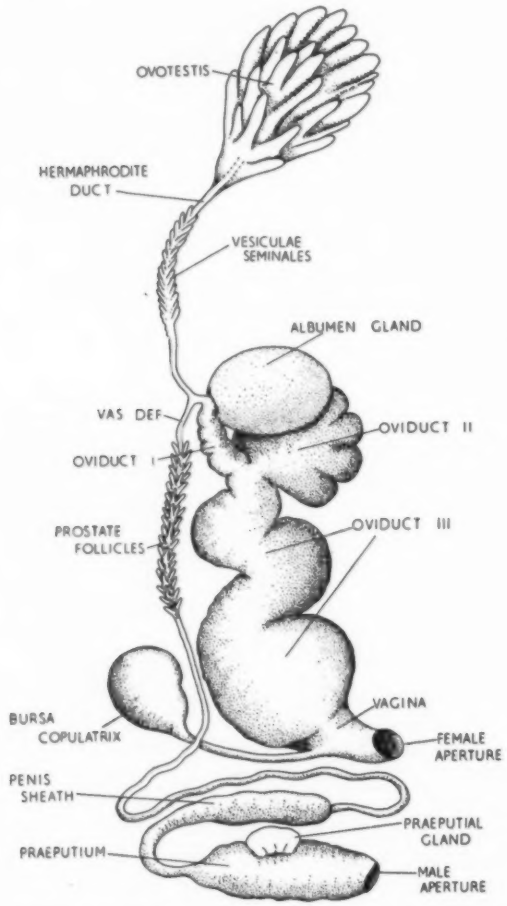


Fig. 1.—Dorsal view of the dissected reproductive organs of *P. fontinalis*.

The genital system of *P. fontinalis* is based on the typical basommatophoran plan, both ova and sperm are produced in the ovotestis and these pass down the common hermaphrodite duct to the point where the male and female systems separate (see Fig. 1). The female duct is formed of the glandular oviduct, divisible into three clearly demarcated regions, and the muscular

vagina which opens to the exterior at the female orifice. Two accessory glands are connected with the female system ; the albumen gland, standing at the junction of the hermophrodite duct with the oviduct and vas deferens, produces the nutrient medium which surrounds the ova ; whilst the bursa copulatrix is a blind diverticulum, the duct of which opens into the vagina. Initially, the vas deferens has many finger-like evaginations, the prostate follicles, opening into it but anteriorly it is a small, muscular duct which enters the penial complex, the penis being enclosed in the penis sheath and opening through the praeputium. The genital system is fully developed during the breeding seasons only, throughout the winter months the male organs are mature but the female tract remains small and does not complete development until the following spring.

The spermatozoa are carried along the vas deferens, receiving the prostatic secretions on the way, and are injected into the copulatory partner by the penis. After copulation, the sperms are stored in the bursa where secretions are added to the semen. The eggs are fertilised whilst still in the hermaphrodite duct either by sperm from the same snail, or by foreign sperm moving out of the bursa and up the oviduct. Investigations in other species disagree as to whether cross- or self-fertilisation occurs and for this reason widely differing functions have been ascribed to the bursa. After fertilisation, the ova each receive a nutritive covering from the albumen gland and then, as they pass down the oviduct, are surrounded by the mucous coats which form the egg capsule.

MATERIAL AND METHODS

Specimens of *Physa fontinalis* were collected in a variety of habitats, but chiefly from ponds and ditches at Stanmore (Middlesex), Lewes Brooks (Sussex) and Loughrigg Tarn (Westmorland), being abundant at all three sites. *Physa acuta*, which was also examined for comparison, was found in the Surrey Canal (Camberwell, London) and specimens were collected from the River Saône in the environs of St. Jean-de-Losne, Côte d'Or, France. Snails were dissected in a saline medium, the formula of which is given by Pantin (1948, p. 67) as being isotonic with the blood of *Lymnaea stagnalis* and the gross morphology was studied. For histological work, a variety of fixatives was tried with varying success, but fixation for eight hours in Susa produced the best results for general purposes.

Following dehydration, clearing in cedarwood oil and embedding, sections were cut at 6 and 8 μ thickness. For general histological and comparative work Heidenhains azan stain proved satisfactory and comparable cells in the reproductive system of the various families of the Basommatophora gave identical results with this stain. For other histological details Heidenhain's iron haematoxylin was used and tests for mucus were made by counterstaining with Alcian Blue (Steedman, 1950) or Southgate's modification of Mayer's mucicarmine (Bolles Lee, 1950, p. 424). All results obtained by these methods were compared with teased preparations of living tissues which were either examined unstained or treated with dilute solutions of neutral red or Janus green B.

The work by Pearse (1953) formed a standard reference for the histochemical investigations, many of the practical details being taken from his appendix. Sections of material previously fixed in 10 per cent neutral formalin were heated in 0·2 per cent ninhydrin as a general test for substances containing amino-acids (Glick, 1949). The periodic acid—Schiff technique (Hotchkiss, 1948) proved satisfactory in the identification of mucopolysaccharides and the dialysed iron method (Hale, 1946), using material fixed in Carnoy, was used as a test for acid mucopolysaccharides. An analysis of the contents of the albumen gland and some other organs was made by the method of paper partition chromatography. Albumen glands were dissected out and placed in small capillary tubes and 0·5 ml. of 2 per cent hydrochloric acid was added. The tubes were then rapidly sealed and heated at 100°C for forty-eight hours, when they were opened and the contents gently warmed until evaporated to dryness. The residue was dissolved in 0·5 ml. of distilled water by very gentle warming ; and the resulting solution was analysed by the standard methods of paper chromatography, as outlined by Block, Durrum & Zweig (1955). Amino acids were detected on the chromatograms by spraying with a 0·25 per cent solution of ninhydrin in acetone and warming the filter paper in an oven. On separate sheets, sugars were detected by spraying the dried paper with aniline hydrogen phthalate and heating at 105°C. for five minutes, when the reducing sugars showed as permanent brown spots (Partridge, 1949).

Experiments were performed to ascertain whether sites of phosphatase activity could be detected in the reproductive organs and dissected snails were fixed for two hours in a solution containing 25 per cent pyridene (12 ml.), 70 per cent ethyl alcohol (17 ml.) and 4 per cent formaldehyde (10 ml.). The specimens were then sectioned and, to determine the cytological position of " alkaline " phosphatase, the procedure and timing described by Danielli (1946) were followed. When testing for the presence of " acid " phosphatase, however, the sections were incubated at 37°C. for four hours in a solution of sodium β-glycerophosphate containing 0·004M lead nitrate buffered at pH 5·0 (following Pearse, 1953, after Gomori). Control experiments, using mammalian material, were conducted when performing the phosphatase detections.

OVOTESTIS

Several workers have studied the ovotestis of various pulmonates, so that the development of the hermaphrodite gland and the cytoplasmic inclusions during gametogenesis are well known and the species studied exhibit a remarkable uniformity in the structure of this organ. Following the earlier work of Blomfield (1881), Ancel (1902) and Gatenby (1917, 1918, 1919), Archie (1942) has produced a detailed study of the cytology and development of the ovotestis of *Lymnaea stagnalis* which closely resembles the conditions found in *Physa fontinalis* during this investigation. Abdel-Malek (1954 a and b) gives a similar account for species in the Planorbidae and Mahoney (1940) has described the extra-nuclear structures found during the spermatogenesis of *Physa gyrina*, the only work on the Physidae in this field.

The ovotestis is a follicular organ, the lobes of which are embedded in the digestive gland and, in a mature snail, contains spermatozoa and ova in all

stages of development. Both types of sex cells develop in the same follicle producing a complex assortment of gametes, although the ova remain attached to the germinal epithelium until mature, while the sperms generally fall into the lumen at an early stage and continue to develop there. Each lobule is bounded externally by an outer Ancel's layer and an inner germinal epithelium. The former is very thin, with nuclei distributed at random along its length and the germinal epithelium is likewise composed of indistinct, flattened cells, although the nuclei are immediately apparent. In some places, especially towards the end of the lobule which unites with the central body of the gland, there is a short tract of lining, ciliated epithelium.

Both male and female gametes develop from the undifferentiated cells of the germinal epithelium. The spermatogonia are produced in clusters, each of which surrounds a Sertoli cell and this is elongated into a stalk extending from the ovotestis wall. The spermatogonia are spheroidal cells, with a prominent, deeply-staining nucleus and these develop into primary spermatocytes by a gradual increase in size. Secondary spermatocytes are formed by reduction division and stages can be found showing meiotic figures. The spermatocytes develop into spermatids when the formation of the tail is initiated by the development of a post-nuclear, cytoplasmic prolongation. This gradually elongates until the typical acorn-head sperm are found in clusters around the flattened Sertoli cell. The mature sperm are united by their heads into plates, their overall length is about 330 μ, although the heads themselves are only 3 μ long.

The ova proliferate from the germinal epithelium and gradually increase in size, reaching at maturity a maximum diameter of about 110 μ. They are surrounded by the nurse cells and in sections these appear as a thin line in which the nuclei are embedded. There are about eleven nurse cells surrounding each ovum, although the number varies considerably within the same snail, and when the egg is mature they disintegrate and disappear.

HERMAPHRODITE DUCT

From the ovotestis, the common hermaphrodite duct conveys both the ova and sperm on the first stage of their journey. Originating within the ovotestis, it soon emerges and runs over the ventral surface of the digestive gland, being chalky-white in colour but partly covered with black pigment. The proximal and distal portions of the duct are thinner, whereas the middle section is more swollen, becoming rather convoluted. This median region has many lateral, digitate evaginations, the vesiculae seminales.

At its anterior and posterior ends, the duct is lined by ciliated epithelium, but throughout most of its length the cilia are confined to a lateral tract which occupies about one-third of the periphery of the lumen. The remainder of the wall of the duct is composed of columnar, glandular cells which also form the secretory elements of the vesiculae seminales. (Fig. 2.)

The ciliated epithelium is composed of small, flattened, cuboidal cells, although at the extreme anterior and posterior (non-glandular) ends of the duct, these become columnar, reaching 40 μ in height. Holm (1946) describes

the vesiculae seminales of *Lymnaea stagnalis* as being of considerable size and having a lumen of about the same magnitude as the duct itself, whereas, in *Physa* these diverticula seem to be an aggregation of glandular cells which have caused a protuberance of the wall of the duct and are the site of extra secretory activity.

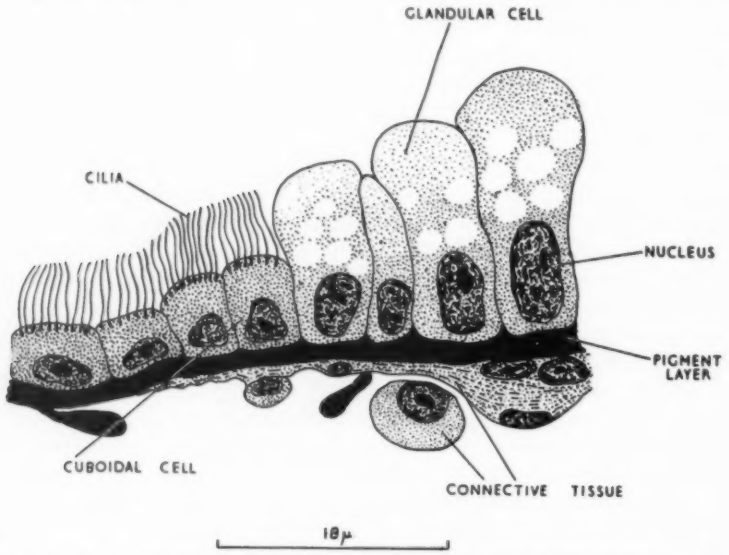


Fig. 2.—*P. fontinalis*. Portion of the wall of the hermaphrodite duct seen in transverse section. Stained with iron haematoxylin.

The hermaphrodite duct is bounded by a thin layer of connective tissue which stains blue with azan and has nuclei interspersed in it. Vesicular cells are to be found attached to this layer. They are conspicuous and elliptical in shape, with a large, centrally-placed nucleus and, lying immediately beneath the epithelial cells, is a characteristic layer of pigment. (Fig. 2.)

On reaching maturity in the ovotestis of a developing snail, the spermatozoa are shed into the hermaphrodite duct which, in sections of all but the smallest snails, is seen to be completely filled with male gametes. When the duct is opened on a slide, the sperm on the periphery of the mass move slowly by undulations of the tail, but the majority remain motionless. It is probable that the short, strong cilia lining the duct are chiefly responsible for transporting the sperm anteriorly, the gametes remaining passive and contributing little by any positive swimming action. The spermatozoa lie in a fluid medium which is secreted by the glandular cells found in the duct and vesiculae seminales. Tests with ninhydrin on sections of the hermaphrodite duct show that this fluid is principally proteinous, although Hale's method also revealed globules of acid mucopolysaccharide material in the glandular cells of the vesiculae seminales. This indicates a nutritive function for the secretions of the hermaphrodite duct. Holm (1946) states that in *Lymnaea*

stagnalis the hermaphrodite duct produces a non-glycogen polysaccharide material and suggests that the secretion " is sufficient to maintain the sperm cells for fertilisation while the secretions of the prostate are chiefly useful as a fluid medium for the transfer of sperm to the female tract during copulation ". Present observations in *P. fontinalis* indicate that sperm is stored in the hermaphrodite duct and passed down the vas deferens only immediately before copulation, which supports Holm's suggestion concerning the different functions of these two secretions.

It is difficult to determine the method by which the eggs pass down the hermaphrodite duct, since an examination of serial sections shows that they move through the centre of the mass of spermatozoa, where the cilia in the duct would have little effect. It is possible that, once liberated from the ovotestis they are capable of amoeboid movement. Thus, the ova of various members of the Hygrophila (Merton, 1924) and of *Philomycus bilineatus* (Ikeda, 1937) have been reported as capable of performing amoeboid movement. However, the ova of *P. fontinalis* contain a large quantity of yolk which would hinder the interconversion of the sol and gel states and it seems unlikely that they are capable of independent motion.

ALBUMEN GLAND

The albumen gland is ovoid in shape and has a granular appearance. Its colour varies from cream (immature condition, found especially in the late autumn and winter) to yellow (breeding condition), and the size of the organ is similarly dependent on the sexual state of the individual. During the period October to February it is small and difficult to detect, being heavily pigmented on its surface and generally obscured by a deposition of fat. The gland lies close to the upper part of the oviduct and the relation between these and the vas deferens and hermaphrodite duct is shown in Fig. 3, which illustrates how the hermaphrodite duct joins the upper end of the vas deferens and then passes into the body of the albumen gland. This junction occurs just outside the albumen gland and the paths taken by the ova and sperms are indicated, the latter being carried down the vas deferens immediately, whilst the former have to pass into the gland to reach the oviduct.

The gland is composed of a great number of secretory follicles which are circular when viewed in cross-section and the whole gland is united within a fine outer bounding membrane. Each follicle possesses a minute, central duct and these unite, ultimately emptying their secretion into the central lumen of the albumen gland. About four to six glandular cells surround the follicular lumen, each with a large and conspicuous nucleus, usually basal in position. (Fig. 4.) The remainder of the cell becomes filled with non-mucus globules which stain deeply with aniline blue. There is a considerable degree of differentiation among the follicles of the albumen gland ; those near the centre are closely packed together and during the breeding season the cells are completely filled with the dark-staining globules, whereas, at the periphery, the follicles are loosely bound together and the cytoplasmic contents of the cells stain less intensely. Here the ground substance of the cell, between the

secretory droplets, is granular and stains pale red with azan. When living material is examined the cells present a similar cytological picture, being filled with clear droplets of secretion.

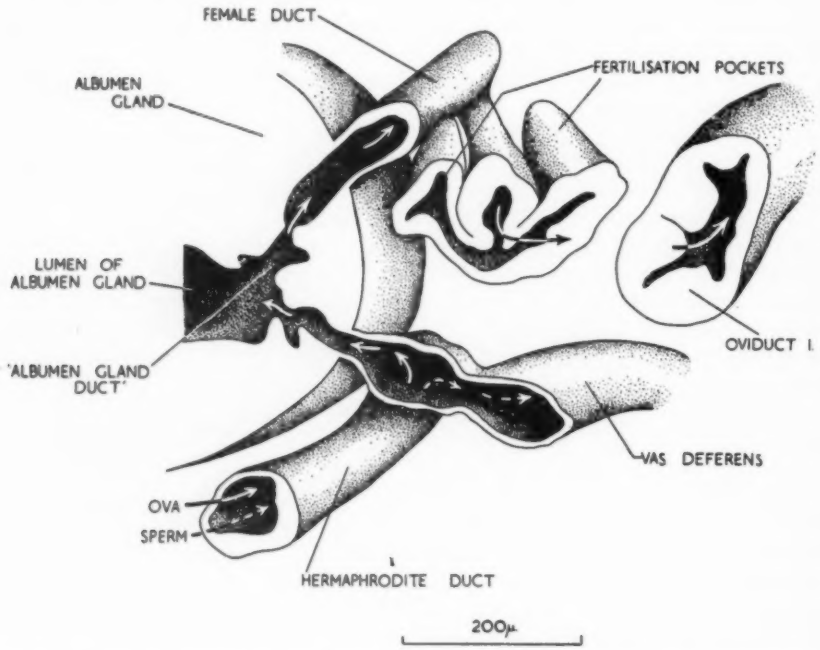


Fig. 3.—Diagram illustrating the path taken by the ova and sperm at the union of the hermaphrodite duct with the male and female systems at the periphery of the albumen gland.

The central lumen of the albumen gland has a complete lining epithelium formed of cuboidal, ciliated cells, about 12 μ high, with a neutral staining reaction. The cilia are difficult to see in fixed preparations, although Gilson's fixative proved the most satisfactory, but are immediately apparent in preparations of living material. The cells rest on a basement membrane and beneath this a fine connective tissue complex can frequently be detected. There are many lateral ducts leading from the central lumen which, initially, are lined with a ciliated epithelium, but this is soon replaced by the characteristic glandular cells of the albumen gland and in this way the central lumen is united with the follicular ducts.

At the junction of the male, female and hermaphrodite ducts, the columnar epithelium is thrown into sphincter-like folds and the whole of this region is surrounded by an extensive muscle sheath. From this point, therefore, the male and female gametes follow separate paths (see Fig. 3) and various explanations have been suggested to account for the mechanism by which this is achieved in different species. Crabb (1927 b), working on *Lymnaea stagnalis appressa*, found, on three occasions, ova which had passed along the male tract

and so, in copulation, had entered the bursa of the partner together with the sperm mass. These ova had no investment of ' albumen ' and must, therefore, have come from the acting male snail. Similarly, I have observed ova in the bursa copulatrix of *Planorbarius corneus* which had no covering of albumen gland secretion ; but after the examination of a large number of specimens, male gametes only were found in the bursae of *Physa fontinalis*. Crabb

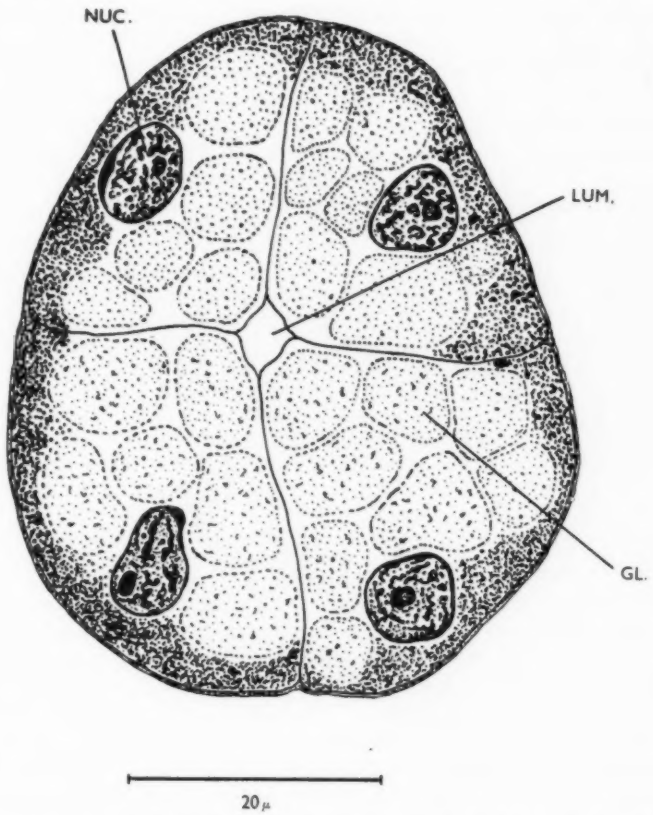


Fig. 4.—Transverse section of a single follicle of the albumen gland of *P. fontinalis*. Fixed Susa, stained with azan. GL.—secretory globule ; LUM.—follicular lumen ; NUC.—nucleus.

found masses of sperm embedded in the ' albumen ' surrounding the eggs of *L. stagnalis* and *L. palustris* which had been bred in isolation and since both male and female gametes may take the wrong path, he concludes that there is no method for their separation. Lacaze-Duthiers (1899) suggests that the oviduct of *Ancylus fluviatilis* is closed when the snail is functioning as a " male", but offers no explanation of its mechanism. Abdel-Malek (1954 a) states that in *Helisoma trivolvis* the oviduct is lined by cilia from its origin at the hermaphrodite duct, whereas, cilia are absent in this region of the vas deferens, an

arrangement which, he suggests, will prevent the ova from entering the male system, although the sperm, which move independently, would be able to pass into the oviduct.

In this investigation, I have found that, in *Physa fontinalis* and *P. acuta*, sperm were often present in the oviduct, even in specimens bred in isolation, which suggests that the separating mechanism, if it exists, is not perfect. At their points of separation from the hermaphrodite duct, both the vas deferens and upper region of the oviduct are strongly ciliated, so that the mechanism suggested by Abdel-Malek in *Helisoma* is impossible in these species. The spermatozoa are probably transported along the male tract in

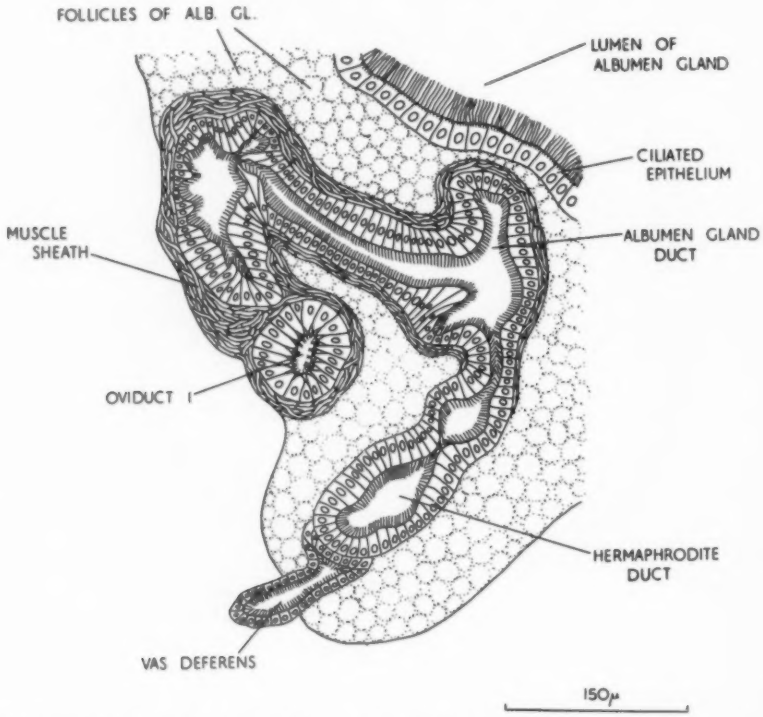


Fig. 5.—Transverse section of the peripheral portion of the albumen gland, illustrating the entry of the hermaphrodite duct and its union with the vas deferens and oviduct. The junction is surrounded by a muscle sheath.

a mass by ciliary action, rather than by their own movements. In *P. fontinalis* and *P. acuta* (Fig. 5) and in the representatives of other families examined, Planorbidae, Lymnaeidae and Ancylidae (Duncan, unpublished observation), the confluence of the ducts is surrounded by an extensive muscle sheath. Although the details of the arrangement at this junction vary in the four families, the muscle sheath is common to all. It seems probable that such a muscular sphincter could serve as a separating mechanism, by closing,

or partially closing, the duct which is not functioning. The sphincter would also serve to retain the spermatozoa within the hermaphrodite duct where they are stored, only permitting their passage into the vas deferens when required. On the other hand, since the eggs are enveloped in sperm when passing along the hermaphrodite duct, a small quantity of the animal's own male gametes will, inevitably, be transferred into the oviduct during the formation of the capsule. This would account for the sperm found in the female duct and also embedded in the 'albumen' surrounding the eggs of *Lymnaea stagnalis* and *L. palustris* (Crabb, 1927 b) and *P. fontinalis* (Wierzejsky, 1905). Eggs were never found in the bursa or anywhere in the male tract in any of the specimens of *P. fontinalis* examined and it is suggested that the sphincter serves to separate all the ova into the oviduct and most of the sperm into the vas deferens. Such a mechanism for the separation of the gametes clearly necessitates complex nervous co-ordination. In contrast to the sperm, eggs are never stored in the hermaphrodite duct and were found there only in snails which had been previously stimulated to oviposit and it is likely, therefore, that they are released from the ovotestis immediately before the formation of the capsule. The liberation of the eggs from the ovotestis could be under hormonal or nervous control. Bretschneider (1948 b) describes the extensive innervation of the genital system of *Lymnaea stagnalis*, which he suggests is necessary to regulate the process involved in the formation of the egg capsule. From these observations it is apparent that considerable co-ordination exists during the reproductive processes and it seems probable that the regulation of the muscle sphincter would not be beyond the limitations of the pulmonate nervous system.

THE MALE SYSTEM

The vas deferens is yellowish-white in colour and follows a somewhat tortuous path to reach the penis on separating from the hermaphrodite duct. Initially it runs beside the oviduct and in this region its dorsal and lateral walls have a large number of blind, finger-like diverticula, yellow in colour. These are the follicles of the prostate which are produced in clusters, branching from the base, although a few are simple. (Fig. 1.)

Close to the base of the oviduct, the vas deferens, still a minute duct, enters the musculature of the body wall, where it passes for a short distance before re-entering the body cavity. Free once again, the vas deferens is a conspicuous, muscular duct, which is coiled above the radular sac before entering the penis. This portion of the vas deferens, together with the penial complex, is enclosed in a common investment of connective tissue, which still, however, permits of considerable movements, both within the body cavity and on the extrusion of the penis.

The vas deferens

The wall of the vas deferens is formed of cuboidal, ciliated cells in which the basal granules are clearly defined. When treated with azan, the cytoplasm stains a bluish-grey, rather more deeply at the base of the cell. The cilia are 18μ long and when living material is examined it can be seen that they

produce a strong current. The duct is surrounded by a very thin connective tissue investment and to the periphery of this are attached the characteristic, ellipsoidal vesicular cells, although the whole sheath disappears in the region of the prostate follicles. There are no muscle fibres in the sheath surrounding the vas deferens in this upper region.

The prostate

The vas deferens is a non-glandular duct which conveys the spermatozoa to the penis, but secretion is added to the semen by the follicles of the prostate. These have a strong ciliation which drives the secretion into the male duct. Although sperm are found in the base of the follicles, they are generally confined to the vas deferens.

At the junction between a follicle and the vas deferens, it can be seen that the structure and function of the two organs are in contrast. Whilst the latter has a ciliated, thin wall with a relatively large central lumen, indicative

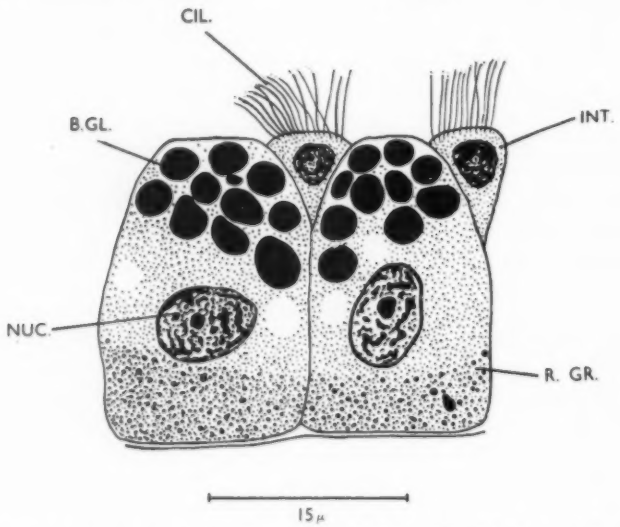


Fig. 6.—Portion of a transverse section of a prostate follicle. Fixed in Susa, stained with azan. B.GL., blue staining globule ; CIL., cilia ; INT., interstitial, ciliated cell ; NUC., nucleus ; R.GR., red staining granules.

of its conducting function, the prostate is formed of glandular cells and the lumen is restricted. The transition of cell types is abrupt, the secretory function of the prostate follicles being evident from the cytology of the component cells. After staining with azan, the cytoplasm may be seen to be differentiated into two regions ; basally it is composed of coarse, reddish-purple granules, whilst at the apical end of the cell, bordering the lumen of the follicle, the cytoplasm is stained blue. As glandular activity reaches its climax, this latter region becomes vacuolated and secretory droplets, which stain a very deep blue, develop. (Fig. 6.)

Wedged between these secretory cells are small, tetrahedral, ciliated cells, discernible with difficulty in sections prepared from fixed material, but immediately apparent in living material. The ciliary current drives the secretions, with which the lumen becomes filled, towards the male duct. The cilia themselves are long and thin and the cytoplasm of these small cells is almost obliterated by the relatively large nucleus. Holm (1946) mentions the presence of the interstitial, wedge-shaped cells in the prostate of *Lymnaea stagnalis*, but does not describe their ciliation, although results suggest that a ciliated prostate is a characteristic feature of all four families of the Hygrophila (Duncan, unpublished observation). This appears to be the first description of their occurrence in any species.

After the periodic acid-Schiff technique, the cells of the distal ends of the follicles usually stain pale mauve and lack the granular inclusions which are characteristic of the cells at the proximal end of the follicle. The fluid which surrounds the sperm in the vas deferens stains positively with ninhydrin, indicating the presence of amino-acids, while polysaccharides were not detected in it. No staining reaction was obtained with the alcian blue test for mucus and chromatograms of the hydrolysed contents of the prostate did not reveal the presence of sugars.

Sections tested for phosphatases showed that, in the genital system, acid phosphatase was localised in the cytoplasm of the ova and in the secretions of the bursa copulatrix (see below). Alkaline phosphatase, however, was detected in the nurse cells of the eggs and in the secretory globules packed in the apical portions of the prostatic cells. In mammals, the acid phosphatase present in the seminal fluid is generally produced in the prostate while the alkaline phosphatase is usually formed in the seminal vesicles (Mann, 1954). Their functions are not clearly known, but the latter may participate in the process of fructose formation. There is no evidence to suggest that, in *P. fontinalis*, it may have a similar role and the prostatic fluid of this species was found to have no apparent effect when mixed with sperm taken from the hermaphrodite duct ; it did not, for example, appear to cause the separation or agglutination of the constituent gametes.

Vas deferens (Distal region)

Once free of the prostate follicles, the vas deferens has muscle fibres in its walls. At this point the ciliated epithelium is very thin indeed, and the muscle coat is not so well developed as it is nearer the penis. As one passes distally, the muscle sheath gradually enlarges and the lumen decreases in diameter until the vas deferens enters the mantle musculature. After running for a short distance within the mantle as a muscular duct, the vas deferens re-enters the body cavity and has now acquired an extensive muscle sheath, whilst the lumen is minute.

The penial complex

The penis is a muscular structure, opening to the exterior on the left-hand side of the head, at the base of the left tentacle. The " penial complex " is composed of the penis itself, which is little more than the continuation of the

vas deferens and is contained within the penis sheath, which can be everted, so that the penis is shot out through the praeputium, a sac-like structure which opens to the exterior at the male genital orifice (Fig. 7). Applied to the surface of the praeputium and opening into its lumen is a glandular organ, the praeputial gland. This was incorrectly termed the prostate by early workers (Slugocka, 1913 and Germain, 1930). The true prostate is common

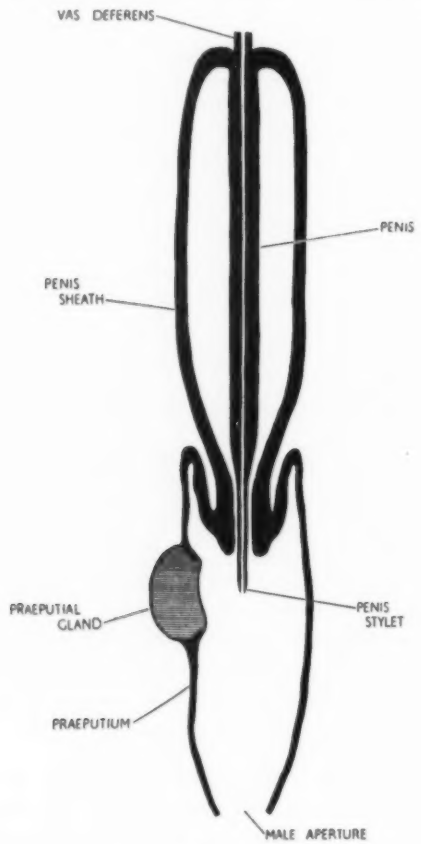


Fig. 7.—Diagrammatic longitudinal section of the penis, penis sheath and praeputium of *P. fontinalis*.

to the four families of the Hygrophila but the praeputial gland is found in the Physidae only and it seems better to reserve the term prostate for the organ which produces the fluid portion of the semen.

The penis is a continuation of the vas deferens, remaining muscular, with an inner circular and an outer longitudinal coat. It is ciliated, but tapers rapidly, becoming very fine. The penis stylet itself contains no muscle fibres and is unciliated.

In non-breeding snails the penis sheath is a muscular tube, composed mainly of circular fibres, and lined by a non-ciliated epithelium. Where the penis sheath fuses with the praeputium, the musculature is modified to form a sphincter and, at the junction, there is a considerable development of glandular cells which closely resemble those found in the praeputial gland. The surrounding epithelial cells in this transitional region between the sheath and praeputium are ciliated, although the secretory cells are nearly as numerous as those of the normal, cuboidal type.

The praeputium is a thin-walled sac with a lining epithelium which is one cell-layer thick and underlying this is a muscle coat composed of short fusiform fibres. The epithelium is ciliated and has goblet cells interspersed at intervals. Characteristic of the praeputium is the praeputial gland, situated towards its proximal end (Fig. 8). It is composed of glandular cells which are flask-shaped

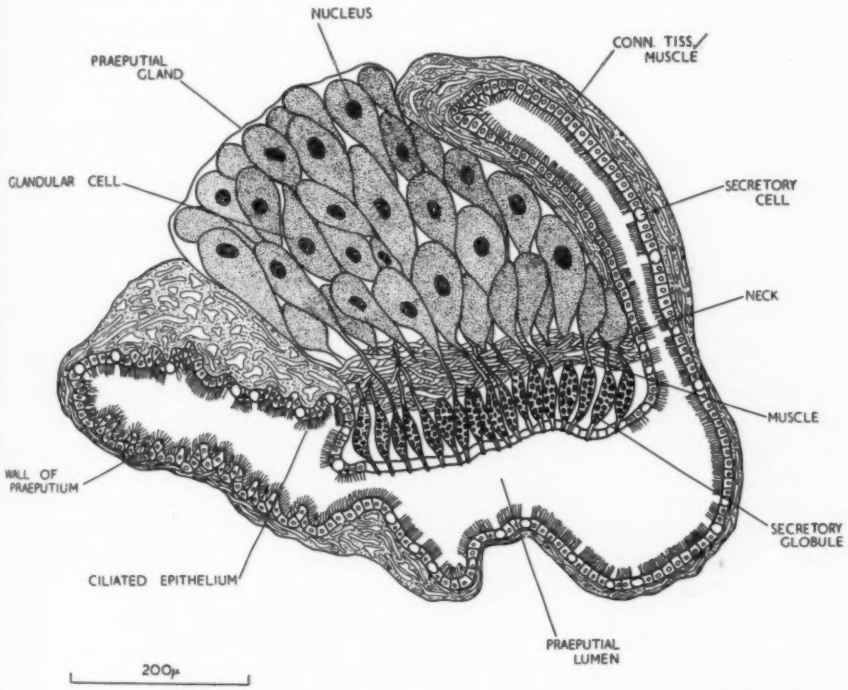


Fig. 8.—Transverse section of the praeputium, showing the praeputial gland. CONN. TISS./ MUSCLE, sheath formed of connective tissue and muscle.

and have greatly elongated necks. The body of each cell has a centrally-placed nucleus surrounded by basophilic cytoplasm which becomes packed with granules and the secretory products are conducted to the praeputial lumen through the elongated cell neck. This is differentiated into two portions ; proximally the neck is thin and running across this region, between the cells, is a band of interwoven muscle strands which presumably act as a

sphincter. Distally, however, the neck is swollen and narrows only slightly to emerge between the epithelial cells. This swollen portion is filled with granular material which stains a much darker blue with azan than the main part of the cell.

Eversion of the penis is effected by the contraction of the protractor muscles and also possibly by the hydrostatic pressure of the blood. During the breeding season, the organ is distended and the layer of glandular cells in the penis sheath is greatly swollen. The penis is everted through the praeputium and the gland cells of the penial complex presumably provide some form of lubrication. After the PAS technique, the glandular cells in the epithelium lining the praeputium stain purple and probably secrete epithelial mucins. A positive result was also given by these cells when tested for acid mucopolysaccharides by Hale's method. The secretory cells of the praeputial gland stain a pale purple colour with the PAS technique, and they and the glandular cells of the penis sheath, in which acid mucopolysaccharides were also detected, produce mucins which presumably facilitate the eversion of the penis.

THE FEMALE DUCT

Oviduct

In the sexually mature snail, the oviduct is swollen and is much larger than the male tract, although, unlike this, it is difficult to see in dissection during the winter months, since at this time it is a narrow, thin-walled duct of minute size (Duncan, 1957 a). When fully developed, the oviduct is bright yellow and several regions are recognisable, although a great deal of confusion exists in the terminology employed for these portions in the literature on the genital systems of the basommatophoran pulmonates. It seems preferable, therefore, to divide the female tract into a glandular oviduct and muscular vagina, subdividing the former into three regions, distinguishable by their anatomy and function :

Oviduct I is little more than a short, narrow conduit leading to the junction of oviducts II and III. The ova pass from the albumen gland into this upper region of the female duct and here there are a number of short, blind diverticula. These are probably analogous to, if not homologous with, the fertilisation pockets described in many pulmonates. (See Fig. 3.)

Oviduct II is a glandular, much-convoluted diverticulum of the female tract, whilst oviduct III forms the major part of the female system and when mature is swollen and distended. (Fig. 1.)

As Holm (1946), working on *Lymnaea stagnalis*, has pointed out, the glandular cells found throughout the oviduct are fundamentally the same, there being a variation from the basic pattern in the different regions. Characteristically, the cells in *P. fontinalis* are tall and columnar, with a centrally placed nucleus (Fig. 9). The cytoplasm is extensively vacuolated and has a mucus-secreting function. Between the cell apices, small, wedge-shaped, ciliated cells with a large, central nucleus are found, their feeble ciliation serving to convey the secretory products towards the centre of the lumen of the duct.

In oviduct I, the columnar cells are rather more swollen than usual and are about 30μ high. They are closely packed together, so making the cell outlines difficult to distinguish and the cytoplasm frequently fails to take up any stain. Initially there is a muscle coat, but this is lost nearer the junction with oviducts II and III. The "fertilisation pockets" are basically similar in histology, but frequently have a muscle coat. Just before joining oviducts II and III, a ciliated tract formed of low, cuboidal cells is developed and this unites with a similar epithelium in oviduct II.

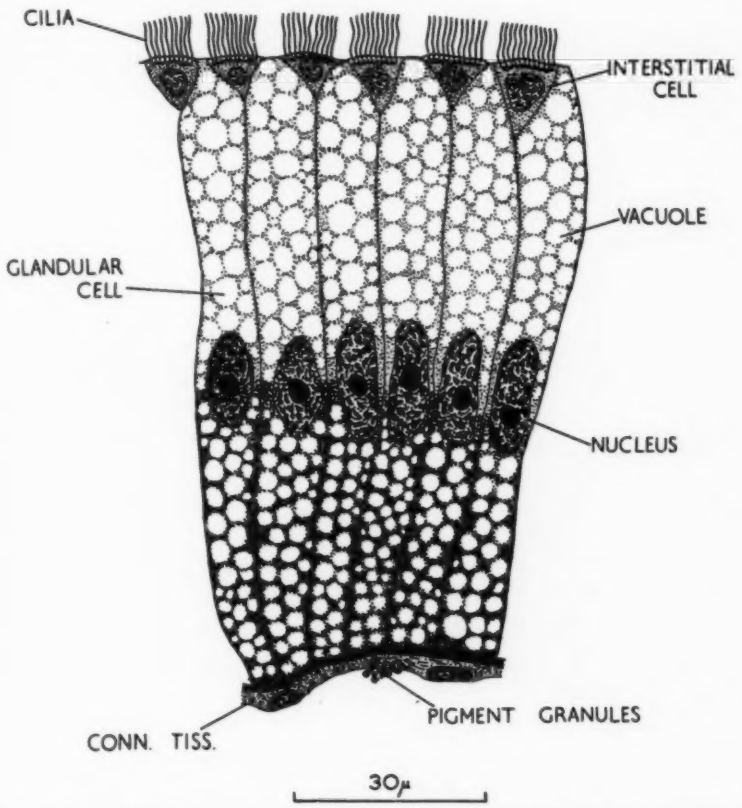


Fig. 9.—Glandular cells with ciliated, interstitial cells, characteristic of the oviduct. Fixed Susa, stained with azan. CONN. TISS., connective tissue.

The extensive development of these tracts of ciliated epithelium is a characteristic feature of oviduct II, a few glandular cells being irregularly interspersed between the cuboidal cells. The glandular cells which comprise the remainder of oviduct II almost always have their cytoplasm differentiated into two regions, the nucleus being centrally placed at the transitional point between the two zones. The apical portion contains clear, vacuolated cytoplasm which stains pale blue with azan but readily takes up mucicarmine,

whereas, the basal portion stains deeply with the aniline blue but gives negative results with mucus-specific stains. The interstitial cells have a large nucleus, relative to cell size. When living tissue is examined, the ciliation is seen to be feeble and it is the tracts of ciliated epithelium formed of cuboidal cells which serve to drive the secretions of the diverticulum out towards the main lumen of the female duct.

The wall of oviduct III is composed entirely of the typical glandular cells, although there are a number of variations of the basic cell type and these tend to occur in definite zones. When stained with azan, the cytoplasm is usually colourless apically with the characteristic basal reticulation, but may be uniformly dark blue or, especially towards the vaginal end, the cells may lose their glandular function. Gradually, at the anterior end, the cells merge into the vaginal type, the interstitial cells are lost and the cells become uniformly ciliated.

Vagina

The vagina is the only portion of the female duct where muscle fibres are greatly developed and it opens on the left-hand side of the animal, a short distance behind the penial aperture and close to the pneumostome. The

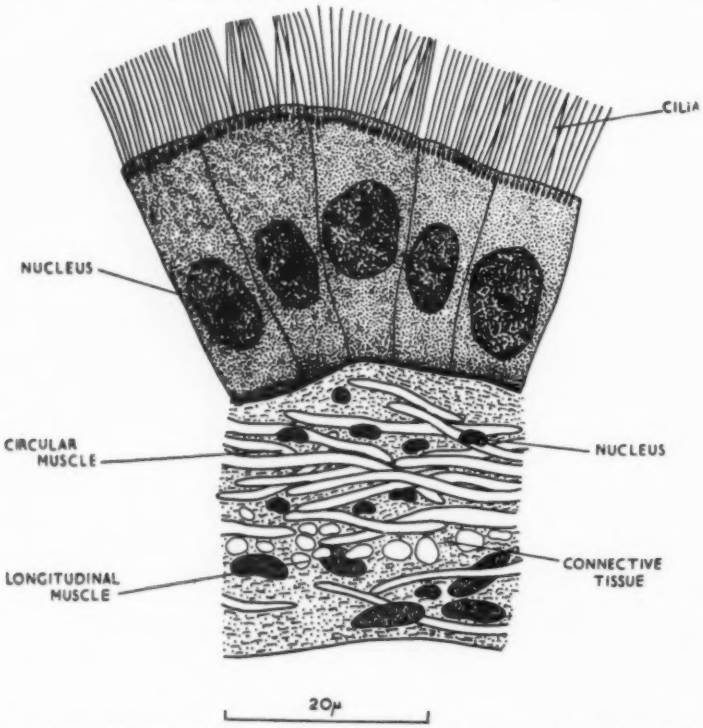


Fig. 10.—Portion of the wall of the vagina seen in transverse section. Fixed Susa, stained with iron haematoxylin.

vagina is composed of ciliated, columnar cells which rest on a thick muscle and connective tissue coat, composed of fibres and vesicular cells. The muscles are differentiated into an inner circular and an outer longitudinal layer (Fig. 10).

THE BURSA COPULATRIX

The female reproductive system of *P. fontinalis* has two accessory organs, the albumen gland described above and the bursa copulatrix, whose duct joins the vagina immediately before it opens to the exterior. It is a thin-walled receptacle, usually appearing bright red in colour, especially during periods of reproductive activity, because its contents are visible through its walls. Situated on the right-hand side of the body, it is usually small, but when filled with sperm and secretion following copulation, it swells considerably, frequently becoming bilobed, although normally it is almost spheroidal in shape. Its duct is fine and muscular.

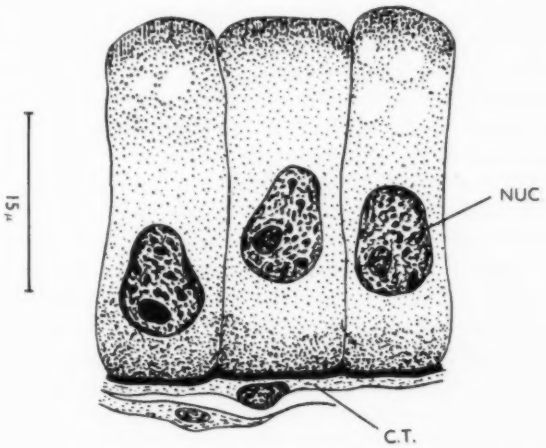


Fig. 11.—Transverse section of a portion of the wall of the bursa copulatrix. Fixed Susa, stained with azan. C.T., connective tissue ; NUC., nucleus.

A wide variety of names has been applied to the bursa in members of the Basommatophora, including seminal receptacle (Holm, 1946, *Lymnaea stagnalis*), receptaculum seminis (Bretschneider, 1948 b, *L. stagnalis*), spermatheca (Baker, 1928 and Hubendick, 1947, surveys of the Basommatophora) and vesicula seminalis (Slugocka, 1913, account of the Physidae). However, Fretter (1941), in her comparative studies of gastropod genital systems, adopted the terminology of calling the storage receptacle, whose duct joins the female system close to its point of opening to the exterior, the bursa copulatrix, whilst reserving the term receptaculum seminis for a diverticulum at the head of the oviduct.

The wall of the bursa is formed of a single layer of cells of the non-ciliated, epithelial type which vary in shape from columnar to cuboidal (Fig. 11).

The epithelium was found to vary in its staining reaction, cells being noted in all stages from intensely acidophilic to neutral, dependent on the maturity and degree of activity of the organ.

After copulation, the bursa is filled with a mass of spermatozoa, of which the heads only are distinguishable, staining bright red with azan. They are embedded in a mass of secretion which is coloured purple by the same stain. Underlying the cells is a conspicuous basement membrane and a connective tissue sheath. The duct of the bursa has a wall which is similarly composed of columnar and cuboidal cells. Muscle fibres are found nearer the female duct, these uniting with the sheath surrounding the vagina. At this junction, the duct of the bursa is ciliated for a short distance, otherwise, however, cilia are absent in the bursa and its duct.

Attempts to fix copulating snails and so determine the position of the penis always failed since, however carefully the operation was performed, fixation caused the penis to retract. Similarly, an attempt was made to cut off the penis during copulation with a pair of scissors, but this also failed. Thus, it was impossible to determine whether it is inserted into the vagina or the duct of the bursa. After copulation, however, the bursa is found to be full of viable sperm which, when the organ is dissected, are capable of slow movement. Sperm may ascend the duct of the bursa by the contractions of its muscular sheath or they may be forced up by the penis at copulation. Alternatively, the sperm themselves may partly assist the process by swimming. The bursa and its duct are non-ciliated, although cilia are found along part of the length of the duct in members of the Planorbidae (Duncan, unpublished observation). Crabb (1927 a) wrongly described cilia in the bursa of *Lymnaea stagnalis*.

The walls of the bursa are glandular and its secretions are added to the semen. An analysis of the secretions is complicated by the difficulty in distinguishing between them and the seminal fluid received in copulation. One substance undoubtedly secreted by the bursa, however, is the characteristic red pigment, which is often found before copulation has occurred. When examined under a spectroscope, the pigment gave no bands characteristic of haem compounds. Subjection to ultraviolet light produced no phosphorescence from the pigment, showing that it was not a porphyrin and the absence of carotenoids was established by its insolubility in acetone and the failure to obtain a blue colouration with sulphuric acid. Since, from these preliminary experiments, the pigment cannot be classified under one of the three main categories of red pigments, haems, porphyrins and carotenoids, it is difficult to suggest what its structure or function may be.

The role of the bursa is still obscure and two functions have been ascribed to it in various species. It may serve as a store for the spermatozoa, secreting substances which assist in their ripening or in the liberation of the individual gametes from the mass. Alternatively, its function may be the histolysis of the sperm entering it at copulation, which may be either all the sperm transferred at this time or merely the excess forced up the duct of the bursa, once the vagina has been filled. If cross-fertilisation is to be effected, the

sperm must either pass up the oviduct directly or re-emerge subsequently from the bursa, since fertilisation occurs at the base of the hermaphrodite duct (see below).

Slugocka (1913) thought that, as the duct of the bursa of *Physa acuta* is unciliated, it would be impossible for the spermatozoa to pass from it into the female tract and so he suggested that its function is the breakdown of the excess male gametes. Crabb (1927 a) states that in *Lymnaea stagnalis* the bursa is a receptacle for free-swimming sperm received in copulation, later to be ejected to the exterior or to disintegrate within four hours if retained within it, the eggs being fertilised by the animal's own sperm. In *Helisoma trivolvis* and *Biomphalaria boissyi*, Abdel-Malek (1954 a and b) states that the sperm leave the bursa and ascend the female tract and it is only those which remain for a long time that undergo considerable disintegration.

Specimens of *P. fontinalis* which I sectioned immediately after copulation invariably failed to show a high concentration of sperms in the oviduct and it must be concluded that the sperm is introduced into the bursa, which was always filled with semen. Subsequent ejection into the water of the foreign sperm was never observed. For twenty-four hours, at least, the sperm contained in the bursa remained healthy and active, although after four days they appeared inanimate. In sections of the bursa, sperm heads were found for some weeks after copulation. Bursa secretion had no apparent effect when added to the sperm taken from the hermaphrodite duct of another snail and it seems probable, therefore, that disintegration, the fate of many sperm, is a natural process and is not assisted by the secretions of the bursa copulatrix.

'Acid' phosphatase is a constituent of mammalian prostatic fluid (Mann, 1954) serving, it is suggested, in the liberation of fructose necessary for the nourishment of the spermatozoa (Pearse, 1953). It is absent in the prostatic secretion of *P. fontinalis*, but sections reveal the presence of acid phosphatase in the contents of the bursa and especially around the free borders of the glandular cells. It seems likely that acid phosphatase fulfils an important role in the physiology of the semen and to acquire this constituent, therefore, the sperm must enter the bursa of another snail. This will favour cross-fertilisation, which is not essential, however, since specimens of *P. fontinalis* bred in isolation are able to produce offspring by self-fertilisation (see below).

To sum up, most of the sperm is received in the bursa, whose secretions include an unknown red pigment and the enzyme acid phosphatase. The functions of neither are clear, but it is possible that the pigment may be an excretory product, while the secretion as a whole may produce a stimulating effect on sperm motility or power of fertilisation. Mann (1954) mentions that, in general, activation by seminal plasma is linked with the occurrence of specific substances in the different accessory gland secretions and it is possible that similar functions may be attributed to them in *Physa*. For example, in certain insects (*Bombyx mori*), the spermatozoa are believed to acquire their full fertilising capacity only after activation by the secretion of the lower portion of the male tract (Wigglesworth, 1950).

FERTILISATION

The arguments in favour of cross- and self-fertilisation in members of the Basommatophora are reviewed in the discussion on p. 79 and conditions existing in the Physidae only are considered at this point.

Under laboratory conditions, *P. fontinalis* is capable of self-fertilisation, since specimens bred in isolation during this investigation produced fertile eggs, although it is difficult to determine to what extent this method of insemination operates under natural conditions. The eggs are generally fertilised in the hermaphrodite duct since, by the time they reach the fertilisation pockets, they have already received the covering of galactogen secreted by the albumen gland. Furthermore, fertilised eggs undergoing division have been found half-way along the hermaphrodite duct. After fertilisation, the eggs change in appearance with the formation of the fertilisation membrane, the irregular outline is lost and they become spherical in shape. Eggs found in the upper portion of the hermaphrodite duct are irregularly shaped, whilst those in the lower regions generally possess a fertilisation membrane. Foreign sperm, to effect fertilisation, will therefore have to pass through the albumen gland and its secretions. This is in contrast to other families of the Hygrophila, where the fertilisation pockets and the albumen gland ducts bear a different relationship to the remainder of the genital system and fertilisation may occur in the hermaphrodite duct or in the fertilisation pockets.

Owing to the difficulty experienced in raising the spat in isolation, it was not found possible to maintain a " line " of *P. fontinalis* propagated by self-fertilisation. However, DeWitt (1954) produced an F_2 generation of *P. gyrina*, although only one individual laid eggs which hatched to produce an F_3 generation. It seems likely that his failure to produce subsequent generations may be due to the gradual build-up of some form of physiological block to self-fertilisation, as has been described in the Tunicata (see Berrill, 1950) and is discussed below. Fertilisation by the animal's own sperm will then become impossible and the entry of foreign sperm will be essential to effect insemination.

During the breeding season, *P. fontinalis* copulates readily when brought into the laboratory, so that it appears that the introduction of foreign sperm is of functional significance. Cross-fertilisation is probably operative in certain cases ; thus, it is tentatively suggested that after about three generations have been produced by self-fertilisation, a physiological barrier to the animal's own sperm is developed, so permitting effective competition by foreign sperm. A study of the morphology and histology of the genital system indicates that, in these cases of cross-fertilisation, the transport of the sperm must be by its own free-swimming motion. The duct of the bursa is long and unciliated and there is no tract of cuboidal, ciliated cells in oviduct III.

SECRETION BY THE ALBUMEN GLAND

Following fertilisation in the hermaphrodite duct, the eggs enter the albumen gland to receive a nutritive investment before passing down the oviduct, where the mucous envelopes which form the egg capsule are added.

In 1938, Baldwin & Bell made an investigation of the secretion of the albumen gland of *Helix pomatia*, which, they found, was composed of a complex galactose polymer. It has been termed galactogen and is similar to glycogen, except that galactose is produced on hydrolysis. Albumen glands of mature *P. fontinalis* were hydrolysed in this investigation with 1 per cent hydrochloric acid and the hydrolysate analysed by paper partition chromatography. The chromatograms, using different solvents, were sprayed with aniline hydrogen phthalate, revealing a single spot in all cases. Identification runs performed beside known sugars showed in all cases that the hydrolysate was composed of galactose. In sections treated with PAS technique, the albumen gland stained a deep purple, whilst no colouration was obtained with iodine. Negative results with Best's carmine showed that the substance secreted was not glycogen. Tests for other constituents in the albumen gland secretion, mucus, proteins, mucopolysaccharides and other sugars, all yielded negative results and it was concluded that the gland produces only a galactose polymer, probably identical with the polysaccharide isolated from *Helix*.

The albumen gland has an almost identical histological appearance in the four limnic families of the Basommatophora (Duncan, unpublished observation) and it is probable that it secretes galactogen in all the members of the Hygrophila. It produces the fluid with which the embryo is surrounded and constitutes its only food supply until hatching. The results of other workers suggest that galactogen is secreted by a wide variety of gastropods and is not peculiar to the pulmonates. It has been found in the albumen glands of *Lymnaea stagnalis* (Holm, 1946), *Viviparus* and *Ariophanta* and in the uterine portion of the oviduct of *Pila* (Meenakshi, 1954). Both workers found a sudden decline in galactogen content after oviposition and also during aestivation.

Bretschneider (1948 b) states that the prismatic cells of the albumen gland of *Lymnaea stagnalis* secrete a fluid " which is chiefly composed of water, proteids and salts ". He distinguishes two types of cells, " gland cells with rather big proteid granules and cells with a large secretion bubble having watery contents ". These results do not agree with Holm's observations on *L. stagnalis* or with the investigations on the albumen glands of other species.

FORMATION OF THE EGG CAPSULE

During their passage down the oviduct, the eggs receive the mucous coats which form the egg capsule and when laid this has a structure which is shown diagrammatically in Fig. 12. Bretschneider (1948 b) has described the method of oviposition in *Lymnaea stagnalis* and Bondesen (1950) has given an account of the egg capsules of the Hygrophila and his terminology is followed in the succeeding description.

In addition to the vitelline membrane, which is the primary envelope, the eggs are surrounded by tertiary envelopes, these being secreted by the female tract. Initially, each ovum and its galactogen is enclosed in two individual investments, the internal and external membranes, the latter being continued to form the egg strings. Bondesen (1950, p. 21) regards the unit formed of the ovum, nutritive fluid and internal membrane as the " egg ". The capsule

is completed by the "eggs" being enclosed within common investments; they are embedded in a less gelatinous substance which is bounded by the capsular membrane. Finally, the completed capsule is covered by the slimy pallium gelatinosum.

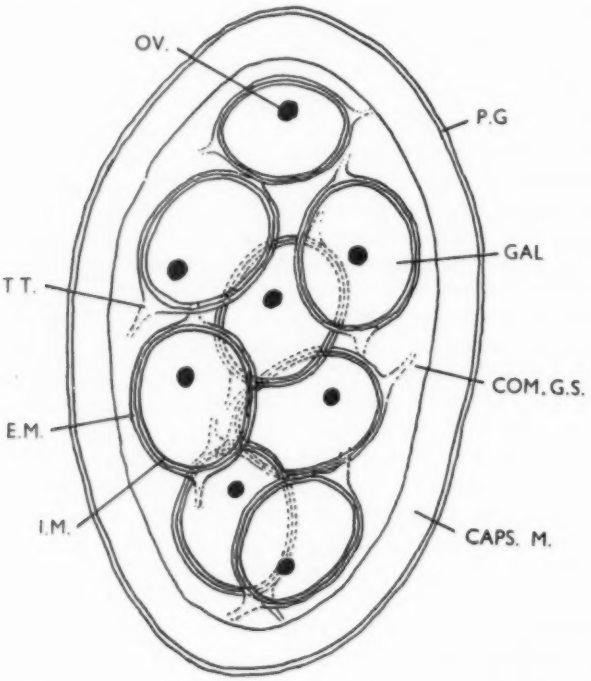


Fig. 12.—Diagram to illustrate the structure of the completed egg capsule. COM.G.S., common ground substance; CAPS.M., capsular membrane; E.M., external membrane; I.M., internal membrane; GAL., galactogen; OV., ovum; P.G., pallium gelatinosum; T.T., terminal tail.

The role of the various parts of the oviduct in the formation of the capsule was investigated by sectioning snails which were fixed whilst the eggs were passing down the oviduct. Individual specimens appeared to vary in the site of deposition of the mucus investments; sections were found with ova in the lumen of oviduct II which were surrounded by galactogen secretion only. However, in general, this is the region of the female duct where the internal and external membranes are secreted and in all cases the individual "eggs" were complete when found in the upper part of oviduct III. In the latter region, the viscous fluid in which the "eggs" are embedded is secreted, together with the bounding capsular membrane. (Fig. 13.) Bondesen (1950, p. 126) supposes that the pallium gelatinosum develops after the capsule is laid and suggests that its formation may be related to the absorption of water.

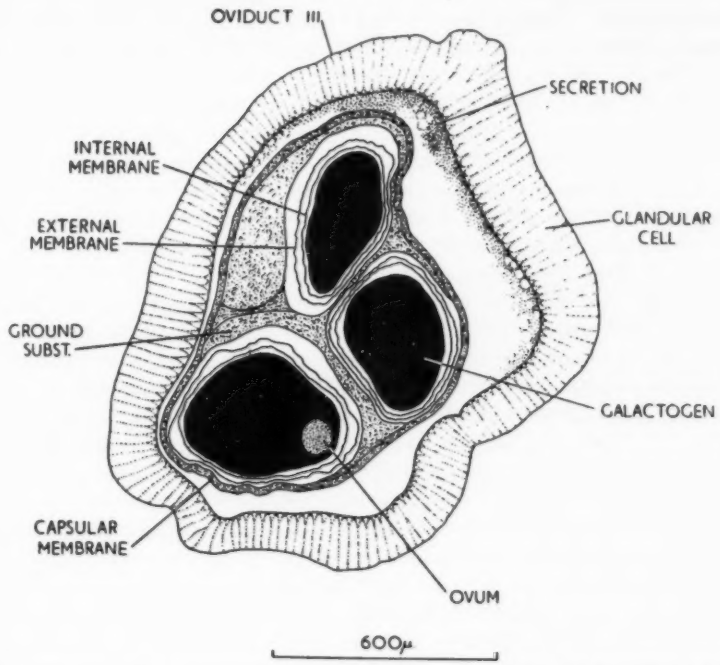


Fig. 13.—Diagrammatic transverse section of oviduct III to show the formation of the egg capsule. From a section stained with iron haematoxylin and alcian blue.

DISCUSSION

Investigations on the reproduction of the freshwater Basommatophora have produced two contrasting schools of thought as to whether cross- or self-fertilisation is the rule. Undoubtedly, the method of fertilisation varies with the species, the individual and the conditions of life, but the most important work has been conducted on the same species by Crabb (1927 a and b, *Lymnaea stagnalis appressa*) and Bretschneider (1948 a and b, *Lymnaea stagnalis*) who describe conflicting results. Crabb believes that the eggs are fertilised by the animal's own sperm, foreign sperm degenerating in the bursa or being ejected, whilst Bretschneider describes how the semen received in copulation has " nutritive " substances added in the bursa and from there the sperm is passed up the oviduct by ciliary action in small balls, to effect fertilisation in the hermaphrodite duct. It would appear to be conclusive from the work of Crabb that the eggs are in fact fertilised and that parthenogenesis does not occur.

The evidence derived from various sources and from different species is briefly reviewed here and in favour of self-fertilisation the following points may be noted :—

(1) Snails bred in isolation from hatching are capable of producing fertile eggs. This has been reported in a number of species, among others, *Lymnaea*

columella (Colton & Pennypacker, 1934), *L. stagnalis* (Crabb, 1927 b), *L. peregra* (Boycott & others 1931), *Biomphalaria boissyi*, *Helisoma trivolvis* (Abdel-Malek, 1954 a and b), *Bulinus contortus* (Brumpt, 1928), *Physa gyrina* (DeWitt, 1954), *Physa sayii* (Crabb, 1927 b) and *P. fontinalis* (see above). Self-copulation is extremely rare and self-fertilisation must occur in these cases.

(2) Larambergue (1937) has established that many natural populations of *Bulinus contortus* are composed of snails which are either aphallic or have only a rudimentary penis. Since self-fertilisation does occur in this species (Brumpt, 1928) in the laboratory, it is likely that such aphallic specimens employ this method of fertilisation under natural conditions.

(3) Except in the Planorbidae, the bursa copulatrix and its duct are unciliated and, therefore, sperms must return to the base of the oviduct either by swimming or by the muscular contractions of the duct or the bursa itself. In *Helisoma trivolvis* (Planorbidae), Abdel-Malek (1954 a) suggests that sperm ascend and descend the duct of the bursa by their own movement and by the action of the cilia which line it. This would necessitate a co-ordination capable of producing a reversal of the ciliary beat.

(4) The oviduct secretes mucus which participates in the formation of the investments which contribute towards the completed capsule, so that if sperm pass up the female duct, they would have to swim through these secretions or travel by the action of the oviducal cilia. Bretschneider (1948 b) describes balls of sperm being carried up the ciliated gutter which lies on one side of the oviduct of *L. stagnalis* and is characteristic of the Lymnaeidae. Such a method of sperm transport, however, could not occur in the Physidae and Ancylidae, where there are no tracts of cuboidal, ciliated cells in the lower regions of the oviduct.

(5) According to Crabb (1927 b), the eggs of *L. stagnalis* are normally fertilised within the ovotestis and further sperm enter as the ova pass down the hermaphrodite duct, polyspermy being the rule. It appears that fertilisation among the Hygrophila may occur in the fertilisation pocket, gonad or the hermaphrodite duct, the last being the most usual. In all the species investigated, the hermaphrodite duct of adult snails was filled with the animal's own sperm and these surround the eggs and so provide competition which will make fertilisation by foreign sperm very difficult.

The evidence presented above appears conclusive, but there are many observations which suggest that cross-fertilisation occurs in many species :—

(1) There appear to be no records of ancylids bred in isolation which have laid fertile eggs. During breeding experiments with isolated *Ancylus fluviatilis*, Bondesen (1950) obtained only a single, deformed capsule which did not contain any eggs. Crabb (1927 b) isolated specimens of *Planorbis trivolvis* for 377 days but obtained only a series of empty capsules.

(2) In *L. peregra*, albino shell colour is a recessive genetic character (Boycott & others, 1931). An albino snail was fertilised by a pigmented (dominant) individual in copulation. The albino specimen was then isolated and the egg capsules which it laid were preserved and the resulting embryos bred. The first laid eggs produced only pigmented offspring, whilst subsequently, the

snails which hatched from later capsules were all albinos. It appears that cross-fertilisation is operative, using the foreign sperm until it is all exhausted, when the ova are self-fertilised.

(3) All species investigated appear to copulate freely during the breeding season and if all the eggs are fertilised by the animal's own sperm, the process of paring would be unnecessary. Copulation might serve as a stimulus to oviposition only (Duncan, 1958), but in this case the secretions of the bursa would be valueless, unless they served in the breakdown of foreign sperm.

(4) Bretschneider has described the process of cross-fertilisation in *L. stagnalis*, in which the sperm pass up the oviduct in the ciliated groove until they reach the hermaphrodite duct where they fertilise the eggs. Based solely on a study of the anatomy of the genital system, such a method of fertilisation suggests itself. The observations are not entirely satisfactory, however, as sperm was frequently found in the oviduct of *P. fontinalis* in specimens which had not copulated and it is likely that such male gametes found in the female system had escaped from the hermaphrodite duct at the junction of the three tracts, due to the inefficiency of the separating mechanism.

(5) Both cross- and self-fertilisation are stated to occur in *Biomphalaria boissyi* (Abdel-Malek, 1954 b). Two different types of ova were found in the fertilisation pocket, (a) those with a regular outline and of the same size as eggs occurring in the ovotestis which were fertilised in the fertilisation pocket and, (b) ova with an irregular outline, slightly larger and undergoing maturation, which had already been fertilised in the hermaphrodite duct. Abdel-Malek suggests that ova of type (a) were fertilised by foreign sperm, whilst those of type (b) were self-fertilised.

It appears, therefore, that the fertilisation mechanism in the limnic families of the Basommatophora can be regarded as extremely variable. Certain species, e.g. members of the Ancylidae and *Planorbis trivolvis*, probably produce ova which may be inseminated by foreign sperm only, whereas, many species regularly self-fertilise their eggs under laboratory conditions with no apparent decrease in capsule production. Between these two extremes, a combination of both methods appears to operate in the majority of snails, as is indicated by the work of Boycott & others (1931) on *L. peregra*. From the results obtained in the present investigation, it has been tentatively suggested that *P. fontinalis* is largely self-fertilising, with cross-fertilisation occurring less frequently and only after the build-up of some form of physiological barrier to the snail's own sperm. However, a further investigation on this subject is necessary and it is hoped to produce more definite conclusions from the results of a series of experiments which have been planned.

ACKNOWLEDGMENT

It is a pleasure to thank Dr J. E. Forrest for his valuable advice and criticism throughout this work.

SUMMARY

Physa fontinalis is a hermaphrodite gastropod in which the gametes formed in the ovotestis pass down the common hermaphrodite duct to the albumen

gland, where the male and female systems separate. The spermatozoa are carried down the vas deferens to the penis and are introduced into the bursa copulatrix of the copulatory partner, whilst the eggs, after fertilisation, pass through the oviduct, where they receive the mucous coverings which form the egg capsule.

The morphology and histology of the reproductive system of *P. fontinalis* have been described, together with an account of the role of each of the genital organs. When mature, the spermatozoa are liberated from the ovotestis and are stored in the hermaphrodite duct, whereas, the eggs are released only immediately before oviposition and pass through the mass of male gametes. It is suggested that the muscle sheath which surrounds the junction of the hermaphrodite duct, vas deferens and oviduct constitutes a regulating mechanism, directing the ova and the majority of the spermatozoa into their correct channels.

The vas deferens is a ciliated, non-glandular duct, but the semen receives secretory additions formed by the prostate follicles, the glandular products being driven out of these diverticula by the action of small, interstitial, ciliated cells. During the breeding season, the characteristic, glandular cells in the penis sheath and praeputial gland become greatly swollen and secrete mucopolysaccharides which probably facilitate the eversion of the penis.

The female duct is composed of a glandular oviduct and muscular vagina, the former being divisible into three regions. The bursa copulatrix serves as a receptacle for foreign sperm and its duct opens into the vagina. Unlike the representatives of the other families of the Hygrophila which have been studied, a true albumen gland duct is missing and the ova pass into the albumen gland before entering the oviduct.

In *P. fontinalis* fertilisation occurs in the lower part of the hermaphrodite duct and not in the " fertilisation pockets ". It appears that the animal is largely self-fertilising, but it is suggested that after several generations have been produced by this means, a physiological barrier to the animal's own sperm is developed, so permitting fertilisation by foreign sperm.

The albumen gland secretes galactogen and, after fertilisation, the ova enter this organ to receive a coating of its nutritive secretion. As the eggs pass down the oviduct, they are surrounded by the mucous envelopes which constitute the egg capsule, each portion of the duct having a separate function in the formation of the different investments.

REFERENCES

ABDEL-MALEK, E. T. (1954 a). Morphological studies on the family Planorbidae (Mollusca : Pulmonata). I—Genital organs of *Helisoma trivolvis* (Say) (Subfam. Helisomatinae F. C. Baker 1945). *Trans. Amer. micr. Soc.* **73**, 103–124.

ABDEL-MALEK, E. T. (1954 b). Morphological studies on the family Planorbidae (Mollusca : Pulmonata). II—The genital organs of *Biomphalaria boissyi*. (Sub-fam. Planorbinae H. A. Pilsbury 1934). *Trans. Amer. micr. Soc.* **73**, 285–296.

ANCEL, P. (1902). Histogénèse et structure de la glande hermaphrodite d'*Helix pomatia* (Linn.). *Arch. Biol., Paris* **19**, 389–654.

ARCHIE, V. E. (1942). The histology and developmental history of the ovotestis of *Lymnaea stagnalis*. Unpublished thesis, University of Wisconsin.

BAKER, F. C. (1928). The freshwater Mollusca of Wisconsin—Pt. I—Gastropoda. *Wisconsin Acad. Sci. Arts and Letters Monograph*—Bull. No. 70 *Wisconsin geol. nat. Hist. Surv.* (Univ. of Illinois).

BALDWIN, E. & BELL, D. J. (1938). Preliminary investigation of galactogen from the albumin glands of *Helix pomatia*. *J. chem. Soc.* **1938,** 1461–5.

BAUDELOT, M. (1863). Recherches sur l'appareil générateur des mollusques gastéropodes. *Ann. Sci. nat. Zool.* (4) **19,** 135–294.

BERRILL, N. J. (1950). *The Tunicata with an account of the British species.* London : Ray Society.

BLOCK, R. J., DURRUM, E. L. & ZWEIG, G. (1955). *A manual of paper chromatography and paper electrophoresis.* New York : Academic Press Inc.

BLOMFIELD, S. E. (1881). The development of the spermatozoa. Pt. II. *Quart. J. micr. Sci.* **21,** 415–431.

BOLLES LEE (1950). *The microtomists' vade-mecum.* 11th edition. Ed. J. Bronte Gatenby & H. W. Beams. London.

BONDESEN, P. (1950). A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods. Hygrophila, Basommatophora, Pulmonata. *Nat. Jutland.* **3,** 1–208.

BOYCOTT, A. E., DIVER, C., GARSTANG, S. & TURNER, F. M. (1931). The inheritance of sinistrality in *Limnaea peregra* (Mollusca, Pulmonata). *Philos. Trans.* (B) **219,** 51–131.

BRETSCHNEIDER, L. H. (1948 a). Insemination in *Limnaea stagnalis* L. *Proc. Acad. Sci. Amst.* **51,** 358–363.

BRETSCHNEIDER, L. H. (1948 b). The mechanism of oviposition in *Limnaea stagnalis* L. *Proc. Acad. Sci. Amst.* **51,** 616–626.

BRUMPT, E. (1928). Étude de l'autofécondation du mollusque aquatique pulmoné, *Bulinus contortus* (L.). *C.R. Acad. Sci., Paris* **186,** 1012–15.

COLTON, H. S. & PENNYPACKER, M. (1934). The results of 20 years of self-fertilisation in the pond snail *Lymnaea columella* Say. *Amer. Nat.* **68,** 129–136.

CRABB, E. D. (1927 a). Anatomy and function of the reproductive system in the snail *Lymnaea appressa* Say. *Biol. Bull. Woods Hole* **53,** 55–66.

CRABB, E. D. (1927 b). The fertilisation process in the snail *Lymnaea stagnalis appessa* Say. *Biol. Bull. Woods Hole* **53,** 67–108.

DANIELLI, J. F. (1946). A critical study of techniques for determining the cytological position of alkaline phosphatase. *J. exp. Biol.* **22,** 110–117.

DEWITT, R. M. (1954). Reproductive capacity in a pulmonate snail (*Physa gyrina* Say). *Amer. Nat.* **88,** 159–164.

DUNCAN, C. J. (1958). The life-cycle and ecology of the freshwater snail *Physa fontinalis* (L.). (In press).

EISIG, H. (1869). Beitrage zur Anatomie und Entwicklungsgeschichte der Gechlechtsorgane von *Lymnaeus*. *Z. wiss. Zool.* **19,** 297–321.

FRETTER, V. (1941). The genital ducts of some British stenoglossan prosobranchs. *J. mar. biol. Ass. U.K.* **25,** 173–211.

GATENBY, J. B. (1917). Cytoplasmic inclusions in germ-cells of snails. Pt. II. *Helix aspersa*. *Quart. J. micr. Sci.* **62,** 555–611.

GATENBY, J. B. (1918). The cytoplasmic inclusions of germ-cells. Pt. III. The spermatogenesis of some other pulmonates. *Quart. J. micr. Sci.* **63,** 197–258.

GATENBY, J. B. (1919). The cytoplasmic inclusions of germ-cells Pt. V. The gametogenesis and early development of *Limnaea stagnalis* (L.), with special reference to the golgi apparatus and the mitochondria. *Quart. J. micr. Sci.* **63,** 445–492.

GERMAIN, L. (1930). Mollusques Terrestres et Fluviatiles. *Faune de France* No. 21.

GLICK, D. (1949). *Techniques of histo- and cyto-chemistry.* New York.

HALE, C. W. (1946). Histochemical demonstration of acid polysaccharides in animal tissues. *Nature, Lond.* **157,** 802.

HOFF, C. C. (1940). Anatomy of the ancylid snail *Ferrissia tarda* (Say.). *Trans. Amer. micr. Soc.* **59,** 224–242.

HOLM, L. W. (1946). Histological and functional studies on the genital tract of *Lymnaea stagnalis appressa* Say. *Trans. Amer. micr. Soc.* **65**, 45–68.

HOTCHKISS, R. D. (1948). A microchemical reaction resulting in the staining of polysaccharide structures in fixed tissue preparations. *Arch. Biochem.* **16**, 131–141.

HUBENDICK, B. (1947). Phylogenetic relations between the higher limnic Basommatophora. *Zool. Bidr. Uppsala* **25**, 141–164.

IKEDA, K. (1937). Cytogenic studies on the self-fetilisation of *Philomycus bilineatus* Bensen. (Studies on hermaphroditism in Pulmonata, II.). *J. Sci. Hiroshima Univ.* (B) Zool. **5**, 67–123.

LACAZE-DUTHIERS, H. de (1899). Des organes de la reproduction de l'*Ancylus fluviatilis*. *Arch. Zool. exp. gén.* (3) **7**, 33–120.

LARAMBERGUE, M. de (1937). Étude génétique de l'aphallie chez *Bulinus* (*Isidora*) *contortus* Mich. *C.R. Acad. Sci., Paris* **205**, 936–938.

MAHONEY, F. J. (1940). Spermatogenesis with special reference to certain extra-nuclear structures in the pulmonate *Physa gyrina* Say. *Univ. Colo. Stud. Gen. Ser.* (A) **26**, 81–83.

MANN, T. (1954). *The biochemistry of the semen.* London : Methuen.

MEENAKSHI, V. R. (1954). Galactogen in some common south Indian gastropods with special reference to *Pila*. *Curr. Sci.* **23**, 301–302.

MERTON, H. (1924). Lebenduntersuchungen an den Zwitterdrusen der Lungenschnecken. Ein Beitrag zur Protoplasma-und Spermiebewegung. *Z. Zell.-u. Gewebelehre* **1**, 671–686.

PANTIN, C. F. A. (1948). *Notes on microscopical technique for zoologists.* Cambridge : Univ. Press.

PARTRIDGE, S. M. (1949). Aniline hydrogen phthalate as a spraying reagent for the chromatography of sugars. *Nature, Lond.* **164**, 443.

PEARSE, A. G. EVERSON (1953). *Histochemistry, theoretical and applied.* London : J. & A. Churchill Ltd.

SLUGOCKA, M. (1913). Recherches sur l'appareil génital des Gastéropodes pulmonés du genre *Physa*. *Rev. suisse Zool.* **21**, 75–109.

STEEDMAN, H. F. (1950). Alcian blue 8 G.S. : A new stain for mucin. *Quart. J. micr. Sci.* **91**, 477.

WIERZEJSKI, A. (1905). Embryologie von *Physa fontinalis* L. *Z. wiss. Zool.* **83**, 502–706.

WIGGLESWORTH, V. B. (1950). *The principles of insect physiology.* 4th ed. London : Methuen.

AN ANALYSIS OF THE TAXONOMIST'S JUDGMENT OF AFFINITY

BY

A. J. CAIN

Department of Zoology and Comparative Anatomy, University Museum, Oxford

AND

G. A. HARRISON

Anthropology Laboratory, Department of Anatomy, University of Liverpool

[Accepted 12th November 1957]

(With 1 figure in the text)

CONTENTS

	Page
Introduction	85
The idea of affinity	86
(i) Different forms	87
(ii) The general plan of an organism	87
(iii) Similarity in general plan	88
(iv) Single characters	89
Analysis of the judgment	90
Discussion	95
Summary	98
Acknowledgments	98
References	98

INTRODUCTION

Whenever a taxonomist (or anyone else) says of three things that on their "overall resemblance" or "general likeness" or some such property, two of them are more closely related to each other than is either to the third, he is making a judgment of *affinity* of an extremely familiar sort. Its familiarity tends to blind us to its remarkable complexity, and this may well be one reason why very few attempts to reduce it to precise formulation have been made. Nevertheless, since it is so frequent a judgment and at present its results are so much a matter of opinion, some attempt should be made in order to make zoological comparison in general and taxonomy in particular more precise.

This paper presents an analysis of what taxonomists do when making a judgment of affinity. The results are summarised in a procedure which can be used for obtaining a numerical estimate of affinity. Since the measurements and calculations necessary are extensive, it is not suggested that it should become a routine technique in ordinary taxonomy, but only that it can be used in doubtful cases, and is of greatest value in clarifying the idea of affinity. Consideration of this procedure shows clearly the limitations of the conventional type of phylogenetic-tree diagram.

THE IDEA OF AFFINITY

The idea of affinity was current in non-evolutionary taxonomy, for example in that of Linnaeus. Here it referred not at all to descent or the possession of a common ancestor, but to *essential* similarity (in the technical logical sense of essential) which was inferred from similarity of parts, properties and attributes and general similarity of plan (Cain, 1958). An estimate of affinity, therefore, was based on the comparison of the general plan of construction of animals or plants, plus all other characters (e.g. of colour-pattern, habits, etc.) that could be observed.

Nowadays we do not search for essences in the Aristotelian sense, but we still use this mode of comparison as a means of determining the degree of affinity of organisms. Affinity in practice means, therefore, degree of overall resemblance estimated from all available characters. Since the coming of evolution, " true " affinity in a phylogenetical sense, i.e. similarity in a number of important characters, as against mere superficial similarity, is explained by the possession of a common proximal ancestor, while superficial similarity is explained by convergence. But these latter ideas are both logically and historically posterior to that of affinity as overall similarity, and are separate from it, as Woodger has already pointed out (1945). Nevertheless, if evolutionary change is by continuous modification, it will be obvious that the more accurately affinity is determined, the more similar will be a classification based on it to one based on the actual phylogeny of a group, if this is determinable. It is not surprising therefore that Darwin was able to take the non-evolutionary classifications of his day, at least those of the best-known groups, and interpret them in evolutionary terms without changing them. Indeed at the present day, since evolutionary lines are not directly observable as such, we still have to classify by affinity and hope that we have a sufficient number of forms available to enable us to connect together those which actually gave rise to each other, however great their resemblances by convergence to other forms.

It is necessary to get some clear idea of affinity at the start, since it is the usual practice nowadays to attempt to base taxonomy on evolution, and the act of estimating affinity can be so involved with that of guessing phylogenetic relationship, that no clear distinction between the two is made. The importance of this distinction has been discussed already (Cain, 1956).

To determine what exactly is meant by degree of affinity, one must know what is meant by

(i) the idea of different forms,

(ii) the general plan of construction of an organism,

(iii) similiarity in this plan,

and (iv) the idea of a single character.

Hardly anyone has discussed the last three ideas, although they are in very general use. Most often they are simply taken for granted or regarded as so simple as to be self-explanatory, which they are not. The most important discussion of the general plan is by Woodger (1945).

(i) *Different forms*

The recognition of different forms can be made in many different ways. The taxonomist may compare, for example, different species recognised as such on biological grounds, different populations definable geographically, strains or ecotypes which can be distinguished by their different ecological preferences or occurrences, or samples of fossils from different localities or strata. And when he says that the degree of sexual dimorphism is greater in one species than in another, he is comparing the sexes within each of two species. Similarly, a remark on the profundity of a metamorphosis presupposes a comparison between successive stages in a single life-cycle. Other comparisons are often made between different polymorphs in the same population, abnormal and normal individuals, a variety of normal ones, or the effects of different allelomorphs on the phenotype within one family of progeny. All these examples have been given because it is easy to forget how various are the comparisons into which the idea of overall resemblance enters. We can conclude that different forms are therefore simply those entities which a taxonomist or anyone else finds it useful to compare in this way. What are compared will depend on his purposes, and so, therefore, will the criteria of difference. Mayr, Linsley & Usinger (1953) give useful discussions of the recognition of some classes of forms usually used by the taxonomist.

(ii) *The general plan of an organism*

This is one of those entities like a spiral staircase—most people are reduced to gestures in the attempt to define it although they may know well what they mean by it, or at least by particular examples of it. Broadly speaking, it may be regarded as the topological relations (irrespective of magnitude) of the parts recognisable in an organism, in as generalised a form as the comparison to be made admits. A classical example of a fairly detailed comparison would be that between a primitive crossopterygian fish and an early tetrapod, of a highly generalized one that between the coelenterates and the rest of the metazoa.

Woodger (1945) in an important paper, has tried to make this and related ideas more precise ; he is elucidating the special features of D'Arcy Thompson's transformations, and it is his section on the general theory of comparison that is relevant to the present paper. His main points are :

In comparing two things " we set up a one-one relation or *correspondence* between the parts of the one and those of the other and proceed to state how corresponding parts resemble or differ from one another with respect to certain sets of properties ".

Further, in working out morphological correspondences " we choose a pairing which will bring the maximum number of parts into identity correspondence with respect to certain of their morphological properties ".

The development of these two points should be studied in Woodger's paper. He shows how for the pentadactyl limb, as an example, every bone can be characterized by means of a few *relations* (including *distal to* and *postaxial to*). The resulting set of morphological relational properties which uses only those

relations with the maximum taxonomic distribution, can be regarded as a general structural plan exemplified in many different forms. Similarly, a plan could be formulated for the whole body of any organism.

It should be noted that such a plan can be based on temporal just as well as spatial relations. The cycles and pathways of synthesis or breakdown in intermediary metabolism which are reviewed by Krebs & Kornberg (1957) can be regarded as chemical systems to be recognised by their constituent series of processes in different organisms. If two animals both possess the citric acid cycle, for example, that is as much a similarity between them as would be the possession by both of pentadactyl limbs. Such cycles and pathways are systems just like morphological systems and can equally be used in the estimation of the overall similarity of two forms.

(iii) *Similarity in general plan*

Woodger is not concerned in the paper just quoted to give a complete analysis of plans and relations, and carefully points out, for example, that the relations brought into being through the loss of parts have not been considered. Consequently his treatment is somewhat static, and does not deal with a gradual change of plan through an evolutionary sequence. However, the extension does not seem difficult in principle.

The point of importance for the present paper is simply that forms may be found of which the general plans differ to any given extent. Any one or more parts may be lost, or differentiated into parts not seen in any other form with the same plan ; any one or more parts may gradually change their spatial and other relations with the remainder. At present it is relatively easy to recognise a certain number of very different plans merely because large numbers of intermediates no longer exist. But if we are to believe the theory of evolution by descent with gradual modification, those intermediates have existed and may even be found as fossils. If we could recover and survey an evolutionary sequence leading from a coelenterate-like form right through to Man, we would be able to choose forms with any degree of difference (within the end-terms) by taking them far enough apart along the sequence. The most similar forms will have the same plans with identical parts and relations, the least will have the fewest parts and relations in common.

But obviously, if any degree of similarity may be encountered, it must be a matter of opinion as to just what degree of similarity is necessary to convince us in the absence of intermediates that one of two forms was descended from the other and not from some third. This point will not be considered further here. We are concerned with the actual estimation of similarity, not its weighting for phyletic purposes.

Woodger's scheme of analysis requires that parts and properties should be recognised, and as he says, " the sets of things and the sets of properties are determined by the particular branch of science with which we are occupied ". The simplest example of a part with properties in taxonomy is the single character existing in different states in different forms.

(iv) *Single characters*

The idea of the single character is of course widely used in taxonomy. In effect it is anything that can be considered as a variable independent of any other thing considered at the same time. For example, in human beings degree of melanization of the skin in mg./sq.cm. is clearly a different character from height, and even if in some races of Man the two were found to be completely correlated, they would still be considered distinct, because a variation in one does not mean by its very definition an automatic variation in the other. But it would be wrong to take as separate characters what are mathematically or logically necessary consequences of each other. In the examination of a human femur, one cannot take as separate characters the lengths of the upper epiphysis, of the shaft, of the lower epiphysis, *and* the total length simultaneously. All that one is doing then is describing the same thing in two different ways. But one could consider total length, length of the shaft, and length of *one* epiphysis simultaneously, since there is no necessary relation between the length of an object and the proportions of the parts into which it is divided. Partial necessary correlation must also be avoided. Degree of melanization of the skin in mg./sq.cm. must not be used together with skin colour estimated by some colorimetric method if the melanin is making a contribution, which is some function of its own density, to the skin colour, unless this contribution can be subtracted from the measurement of skin colour.

The situation is different when a character depends on the presence of another one to be developed at all, because it is a qualification of that other. For example, if there is an outgrowth on the beak of a bird, that outgrowth may be spherical, lamellar, smooth, serrated, tubercled, and so on, but none of these characters of shape can be observed if there is no such outgrowth. When the outgrowth is present, they can be treated as independent variables of various values, but when it is absent they cannot be given the value 0. They are then simply *inapplicable*.

In considering simple affinity, one must score only characters which are independent in the sense explained above. Of course many characters are far from independent in the statistical sense, since they may be *functionally correlated*, or the mode of life of an organism may require their simultaneous presence ; in this case they are *ecologically correlated*. For example, a biting canine in the lower jaw requires sharp edges to bite against in the upper jaw ; and an arboreal leaf-eater must have both climbing appendages and the appropriate form of gut. However these correlations, although of great importance in weighting similarities in an attempt to guess phylogeny, are not relevant when we are trying to work out the degree of overall similarity of two forms. They must be considered when this degree of similarity, whatever its value may be, is to be explained in evolutionary terms.

Consequently, all characters which are not mathematically necessary correlates of each other may be considered as independent for the purpose of estimating overall resemblance, whether they are functionally or ecologically correlated or not. We must also be sure that we are comparing the same character in different forms. The general plan must be known before it can

be said that we are doing so. Le Gros Clark (1955) gives an excellent example. The maximum height of the human skull measured in the Frankfurt plane from the auditory aperture is an index in Man of the height of the brain case. If the same measurement is taken in the gorilla it includes both the height of the brain case and of the sagittal crest, which is often huge in males. Consequently, as Le Gros Clark says, the two measurements are not morphologically equivalent. Here we must consult the general plan of each form. Two parts in two organisms are said to be morphologically the same if they are corresponding parts within a single structural plan, showing the same relations with other parts also recognisable as elements of the plan. (As mentioned above, there may well be examples in which the degree of similarity is so low that there is considerable doubt as to what in one form corresponds to what in another).

Mayr has said (1942) that the number of characters is limited only by the patience of the investigator. In practice this is true, and in consequence taxonomists use some rule of economy in their procedures. It is customary to say of two forms that they are identical as far as is known *except* in the characters w, x, y, etc. It is then unnecessary to measure thousands of characters in which these two are indeed for the purposes of the investigation identical. Similarly, it is usual to measure these characters in such a way as to express as much of their differences as possible in a single measurement. For example, if two bones were identical in shape but different in absolute size, no doubt all sorts of different lengths between points could be measured on both and treated as separate characters ; but it would be simpler to say that one bone was the same shape as the other but with total length 1·36 times greater. It is here that complexes of characters which are functional or ecological correlates are useful, since as long as only those forms are compared which have the complex in question, it can be represented by the value of any single character in it, preferably that which is easiest to measure.

In general, the terms used should sum up as many characters as possible, for completeness of description, as long as those subsumed under each term remain constant or correlated with each other. If however in any form they vary independently, they must be described separately.

ANALYSIS OF THE JUDGMENT

In making his judgment, the taxonomist says something like " These two forms differ in very few characters, and then only slightly ; they differ sharply from the third but only in one character, so I think they must be regarded as close to it, though not as close as to each other. But they differ from the fourth and fifth (themselves closely allied) in every character I have studied. These two last must therefore form a group distinct from the other three ". In other words, he is summing up in some way all the differences between any two forms at a time, irrespective of what units they are expressed in, and is using the total as his measure of overall difference, which is readily convertible to a measure of overall likeness or affinity.

Such a judgment presupposes that he has already recognised the general plans of all the forms dealt with (as indeed an experienced taxonomist would) and is confident that the characters he is considering are both independent of

each other and the same in all the forms. What is involved in this has been indicated in the previous section of this paper. We can now see how the values of the characters can be combined.

Let us assume at first for simplicity's sake that each character in each form can be represented by a single value. (Exactly how this is obtained, and which among several alternatives should be preferred, is a practical question not dealt with in this paper.) Obviously, the first step must be to get rid of the actual units of measurement, which may bias the values. It is a *difference* in size in two forms, for example, which interests the taxonomist, not whether the size is measured in centimetres, micra or feet. This can be done most readily by transforming each value to a pure number, using division by another quantity in the same units. The simplest method is to divide all the values observed for a character in the forms investigated, by one of those values. The resulting numbers may be called the *reduced values*. Use of the maximum value so far observed ensures that the values of all the characters are brought to the same scale, the maximum being always 1. This means that if a form is discovered which has a greater value for any character than has been observed before, the reduced values for that character must be recalculated throughout since there is now a new unreduced maximum. However, this seems to agree with the usual taxonomic practice. A group in which there is marked variation of a particular character is considered rather heterogeneous in respect of that character. If now a new form is discovered which obviously belongs next to the group but has a far higher value for this character than has been observed so far, it will stand away from the other forms in this respect, and they will now appear to be a more homogeneous group. The necessary recalculation will take this change into account.

This method of combination of values allows us to take into consideration all characters, whether lengths, weights, colours, items in a behaviour pattern or simple presences and absences. This is obviously what the taxonomist does.

As mentioned above, it is necessary to distinguish those forms which do not have a particular character from those in which it is present with value 0. This is readily done when one character is a qualification of another, but is more difficult in other situations. When the general plan has been recognised, a particular character can be identified in any form which has it, by its relations in the general plan. (This may of course require considerable research ; it is only comparatively recently in the history of comparative anatomy that the homologies of the ossicles of the mammalian ear have been worked out). Now if a particular character is absent in one form but the rest of the general plan seen in the other forms that have this character is present, it may be reasonable to consider that since all the relations of this character with others are possible in this form, the character is present but with value 0. To take an example, the earliest titanotheres had no horns. In them the nasal bones, although of course present, were not specially thickened. In later forms, progressively larger horns were developed as thickenings of the nasals. Since the early titanotheres are so similar to the later ones, it is reasonable to consider that in effect they had undeveloped horns, and to score them for this character as 0. Some later titanotheres had simple horns, some forked ones, so that for them

horn shape can also be used as a character. This, however, is unscorable if the horns are absent or undeveloped. For such forms it is inapplicable, and cannot be given any value. Sometimes it may be impossible to decide whether a character is inapplicable or of value 0. Such situations are discussed later (p. 94).

With the above points in mind we can now see how a combined value for the differences between two forms is obtainable. First, one recognises the different forms appropriate to one's investigation, and examines their general plans. Next, one measures the same characters in all the forms to be investigated, putting 0 where the character is present but undeveloped, and leaving a blank where it is inapplicable. This is most conveniently done by making a table with columns for the forms and rows for the characters. Thirdly, all the values for each character are divided through by the maximum observed value for that character ; this gives the reduced values and removes the bias produced by the different units of measurement. Fourthly, a second table is made, in which each column contains the differences between the reduced values of each character, for two of the forms ; all the forms are thus compared with each other two at a time. Lastly, the total of the reduced value differences for each pair of forms (the result of adding up each column) is divided by the number of characters used in the comparison, to give the *mean character difference* between two forms. This is necessary because all the characters may not be applicable in all the forms, and the total number of characters used may differ from one pair of forms to another. We consider that this procedure is an adequate analysis of the considerations which a taxonomist uses, as epitomised at the beginning of this section. Tables 1 and 2 show the working of a dummy example.

Table 1 shows the reduced values (to obviate a multiplicity of decimal points, they have been multiplied by 100 throughout) of characters (1) to (7) as measured in forms A to E inclusive. Inspection of this table will show at once that A, B and C are very alike, and different from D and E which resemble each other closely. In characters (4) and (7) occur values of 0, while characters (5) and (6) are inapplicable in some forms. There is no doubt on the evidence given that we have two groups, A, B and C on the one hand and D and E on the other. Table 2 is the difference table constructed from Table 1, and is headed for all the forms taken two at a time. Where a character is inapplicable to a given form, that form has no value for it, and consequently no difference in the compartments of that row. At the bottom are given the mean character differences, which entirely confirm the taxonomic judgment, but give precise measures for the differences between all the forms.

No special taxonomic significance attaches to the sum or the mean of the reduced values for each form, and neither is a good guide to its taxonomic position, as can be readily seen from Table 3. It is obvious from the reduced values given here that we have two well-marked groups, A, B and C on the one hand and D, E and F on the other. Yet the totals of the reduced values are the same for all, and since the same number of characters is compared throughout, the mean reduced values are also the same. But the difference table (Table 4) shows the grouping clearly.

TABLE 1

	A	B	C	D	E
(1)	100	90	95	5	10
(2)	100	85	80	5	5
(3)	75	100	95	20	15
(4)	5	5	0	80	100
(5)	90	100	—	20	25
(6)	100	50	25	—	—
(7)	90	95	100	0	0

TABLE 2

	AB	AC	AD	AE	BC	BD	BE	CD	CE	DE
(1)	10	5	95	90	5	85	80	90	85	5
(2)	15	20	95	95	5	80	80	75	75	0
(3)	25	20	55	60	5	80	85	75	80	5
(4)	0	5	75	95	5	75	95	80	100	20
(5)	10	—	70	65	—	80	75	—	—	5
(6)	50	75	—	—	25	—	—	—	—	—
(7)	5	10	90	90	5	95	95	100	100	0
	115	135	480	495	50	495	510	420	440	35
	7	6	6	6	6	6	6	5	5	6
	16·4	22·5	80·0	82·5	8·3	82·5	85·0	84·0	88·0	5·8

TABLE 3

	A	B	C	D	E	F
(1)	100	100	100	0	0	0
(2)	100	100	100	0	0	0
(3)	0	0	0	100	100	100
(4)	0	0	0	100	100	100
	200	200	200	200	200	200

TABLE 4

	AB	AC	BC	AD	AE	AF	BD	BE	BF	CD	CE	CF	DE	DF	EF
(1)	0	0	0	100	100	100	100	100	100	100	100	100	0	0	0
(2)	0	0	0	100	100	100	100	100	100	100	100	100	0	0	0

and so on

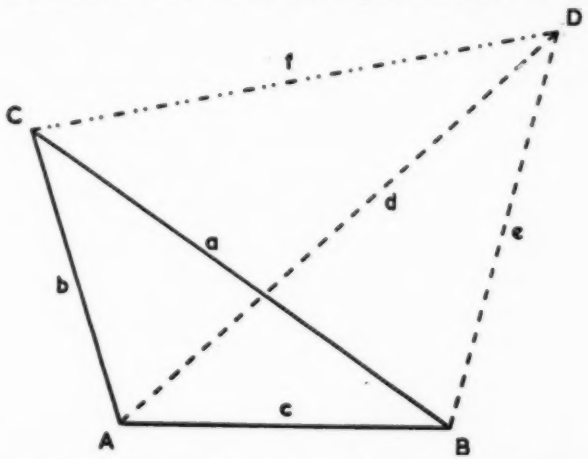
The question remains, what relation does the mean character difference bear to the affinity between two forms. Now, if two forms differed only very slightly in all the characters observed (the most extreme of sibling species, for example) all the differences would approximate to 0 as would the mean character difference. If on the other hand, in all the characters compared, one form had the highest known value and in the other it was 0, the mean character difference must be 1. Consequently, the degree of affinity can be expressed as 1—the mean character difference, being very nearly 1 in the first example just discussed and 0 in the second, for the characters considered.

We can now return to the situation mentioned above, in which it is uncertain whether a character should be regarded as inapplicable or of value 0. For example horses and rhinoceroses are fairly closely related. No horses and no running rhinoceroses (which were necessarily lightly built) developed facial horns, but the heavier rhinoceroses produced the well-known epidermal "horns". If any horse had become slow and heavy, not taking to its heels to avoid enemies, it is quite possible that it might also have developed horns of the rhinoceratoid type, but this is something of which we can never be certain. If in a comparison within the perissodactyls one scores for presence of the rhinoceratoid horn and puts 0 for the horses as well as the running rhinoceroses, the effect, as can be seen from a consideration of Table 1, will be to add one more character to those applicable to the horses, thereby reducing the mean character difference between them and the rhinoceroses (since the additional character has the value 0). If, as is usual, the investigation is being made to find out the natural groupings, it will always be safer in doubtful cases to regard a character as inapplicable since this will not reduce the mean character difference and thereby raise the affinity correspondingly, thus suggesting that the forms concerned are more closely related than the evidence warrants.

Now we can remove the limitation to a single value for each character in each form. Most usually all we have is an estimate based on a sample of each form, and it is necessary to determine statistically the most probable value for the character. None of the usual statistics are affected by the procedure given in this paper, which involves only the dividing through of the raw data for each character by the most probable value for the highest expression of that character. We shall have for each value of a character a number and a range according to the size and variability of the sample and the level of probability taken. All that is necessary is to enter into the appropriate compartment of the table of reduced values, both the maximum and the minimum likely values on the available data and to use both in calculating the differences table. Then the final mean character difference or M.C.D. for each pair of forms will lie between that found by using the maximum values of all the character differences in that column, and that found by using the minimum values. This complicates the tables somewhat but introduces no departures in principle. (In usual taxonomic practice, when the values for a character in different forms are markedly different with no overlapping, and the uncertainty about each is slight, most people would use a single value, usually the mean, in each compartment of the table of reduced values.)

DISCUSSION

The formulation of this analysis allows us to resolve one important problem forthwith. It is always difficult to make sure exactly what is meant by a phylogenetic tree diagram. In one sense the meaning is obvious—everything represented by a branch arising from another one has descended from ancestors represented at the point of junction, which themselves were produced later than those represented at the junction of the earlier branch and the trunk, and so on. These phyletic relationships have been described as the *evolutionary topology* of the group in question (Cain, 1956), and family tree diagrams show them well. The difficulty arises when one tries to make the length of a branch or its angle of divergence from another represent amount of evolutionary divergence. This is frequently done but never with success quantitatively. The analysis given in this paper shows why. Since there is no necessary connection between the values of a character in one form and in another, still less between the values of different characters in the same form, it follows that there is no relation between the M.C.D.s of different pairs of forms. Now if three forms are closely related, all the M.C.D.s are likely to be of similar values, and the sum of any two will be larger than the third. Consequently they can be represented as the sides of a triangle with the forms at the corners.



This situation is shown in Fig. 1. Now, a similar construction will give a triangle for two of these original forms, say A and B, and a fourth, D, and this triangle will share one side with the first. But however these two triangles are rotated using their shared side as axis, it does not follow that the distance between C and D will ever be the appropriate value to represent their M.C.D. The relation between this distance and the others representing M.C.D.s in Fig. 1 is a very definite one, being in fact for the maximum and minimum values of f,

$$f^2 = b^2+d^2-2bd \cos (C\hat{A}B \mp D\hat{A}B)$$

where $\cos C\hat{A}B = (c^2+b^2-a^2)/2bc$

and $\cos D\hat{A}B = (c^2+d^2-e^2)/2cd$

The chances of this relation being correctly fulfilled by a value of f bearing no necessary relation to those of the other sides of the figure are negligible. Consequently we can say that although the mutual differences (and therefore similarities) of three forms can usually be represented by a diagram in two dimensions, those of four cannot necessarily be represented by one diagram even in three dimensions, let alone in two. Perhaps the use of additional dimensions for every new form might help, but it seems doubtful.

This means, then, that the successive forms recognised along a phyletic line may each be represented in a phyletic diagram at the right distance from its two immediate neighbours to represent its M.C.D.s with them ; but it will not then be at the right distances from other forms on the same line. It is true that the reduced values for any single character in several forms can be correctly represented along one straight line from 0 to 1, but M.C.D.s cannot be treated in this sort of way. The attempt to use phyletic diagrams to express anything other than plain evolutionary topology, therefore, by the very nature of our ideas of overall similarity and difference is hopeless and can at best produce only an approximation of very uncertain value, perhaps materially misleading.

Secondly, we can now express precisely the taxonomic *relevance* of particular comparisons. Two birds can be compared in the minutest detail since all birds are comparatively similar, but an echinoderm and a tapeworm have very little in common. This means that most of the characters in one are simply inapplicable in the other. The *relevance* of a comparison can be easily expressed by the ratio of twice the number of applicable characters considered (since these are shown by both forms) to the number of inapplicable ones (each of which will be shown by only one of the forms).

It will be seen that the procedure for estimating affinity worked out in this paper supposes that the forms to be compared can be distinguished on some basis, and that they will often be distinguished on evidence which does not enter into the tables of comparison at all. The criterion for biospecific distinctness, for example, is whether or not two groups of individuals interbreed freely in the wild, completely irrespective of their morphological characters. Similarly, the criteria for whether or not two forms are due to different allelomorphs of the same gene, are based on genetical experiments, not at all on the characters of the phenotypes in question. The produre, therefore, has nothing in common with those statistical procedures which give the probability that a sample is drawn from a particular population, or estimate a population's characters from samples.

The formulation of this procedure has required many discussions between us over the past three years, and the principal difficulty we have found was to separate out the plain estimation of the affinity of two forms, and the weighting of the results to give some phylogenetic interpretation. It is so easy and so usual for the taxonomist to look at a new form, appreciate at a glance its general plan and peculiarities, immediately ignore some striking character because on the basis of his past experience he knows it is very liable to change from species to species in this group, discount another because it is functionally bound up in this group with a third and will therefore evolve with it *pari*

passu, and seize on a fourth as especially important because on any one or more of many different grounds, rational or emotional, severely analytical or wholly traditional, he believes it to be primitive. It is not surprising, therefore, that the two remarkable features of the procedure, namely the very wide interpretation given to independence of characters, and the lack of any reference to genetical evidence as such, are both due to the disentangling of phylogenetic weighting from estimation of affinity.

If several characters are controlled by a single gene, then, however striking they are, they are regarded as of comparatively little importance. " Importance " is one of the worst words in taxonomy, since it has a multiplicity of meanings which are seldom made explicit. Now a little reflection will show that in this example all that is meant is that since these characters are controlled by a single gene, they are liable to change very easily, and will all change together, consequently they are of little importance in guessing phylogenetic relations. But this is irrelevant when we are estimating how different the form with them is from that carrying a different allelomorph ; furthermore, when effects are said to be due to a single gene, we really mean that the rest of the genotype is carefully buffered so that the allelomorphs at this locus always produce certain effects—we cannot assert that these effects *necessarily* follow from the action of each allelomorph, since we know that they can be modified by other genes. That particular effects all depend usually on a single locus in one form but on many in another, therefore, may affect our genetical or phylogenetical classification of these forms, but does not affect the procedure when we compare them to obtain their M.C.D.s. If the evidence can be quantified it can be used in the tables in rows for characters of the genetic systems of the forms.

Similarly, when we wish to know just how alike or how different two forms are, we are not concerned to know whether two characters are functionally or ecologically correlated. The implication is that because they are correlated we shall *always* find one of them in every form in which we find the other. This obviously has considerable importance in phylogenetical speculation, but not in an estimate of affinity. (Moreover, it is very seldom that we can assert two characters to be *necessarily* functionally related, so that they will always go together. We are always supposing that the conditions of life of the organism concerned are remaining effectively constant. The cutting edges of the canines were given above as a good example of functional correlation. But in the sabre-toothed tiger *Machairodus* and in its marsupial analogue *Thylacosmilus*, the upper canine has cutting edges which do not work against edges in the lower canine since they are now used for stabbing. The one does not always presuppose the other).

Although the procedure requires considerable measurement and calculation, and is not likely to be used for routine taxonomic work, it offers one possibility which requires serious consideration. For a given number of characters determined on adequate samples in each form investigated, a precise M.C.D. can be calculated for every pair of forms The more characters investigated, the more the M.C.D. for a pair is likely to approximate to a fairly constant value. It should now be possible to give a quantitative mean-

ing to the taxonomic hierarchy. In the simplest case, consider a large number of species with no sexual dimorphism and differing most in their adult stages, the comparison of which will therefore be sufficient. If their M.C.D.s are worked out on a reasonably large number of characters, it should be possible to agree on a M.C.D. value at the generic level, such that if a group is formed of species all of whose M.C.D.s are lower than this value, they are to be regarded as in the same genus ; but a species which has M.C.D.s with the species in the group of higher values must be put into a neighbouring genus. Such suggestions must be given careful examination, and it is necessary that a number of accepted groupings of different ranks should be examined with the aid of the procedure given in this paper before any tentative proposal is made. But the prospect of a quantitatively-based hierarchy is at least encouraging.

SUMMARY

1. The basic idea of affinity as overall similarity, which is logically and historically prior to that of evolutionary affinity, is described. It is in constant use in taxonomy.

2. After an analysis of the ideas of different forms, the general plan of construction of an organism, similarity in general plan, and the single character, a procedure is worked out which makes precise the judgment of affinity, and enables us to obtain a numerical value for the mean character difference between any two forms.

3. As a result, it is shown that the family tree diagram can be used only for the evolutionary topology of a group, not for showing amount of evolutionary difference.

4. A measure of the *relevance* of a taxonomic comparison is described.

5. The possibility of giving a quantitative basis to the taxonomic hierarchy is pointed out.

ACKNOWLEDGMENTS

We are indebted for criticism and other help to Mrs J. T. Cain, Dr P. M. Sheppard, Dr P. C. J. Brunet, and Messrs B. C. Clarke, J. D. Currey, J. Gurdon, D. Nichols, H. K. Pusey and M. H. Williamson.

REFERENCES

Cain, A. J. (1956). The genus in evolutionary taxonomy. *Syst. Zool.* **5**, 97.

Cain, A. J. (1958). Logic and memory in Linnaeus's system of taxonomy. *Proc. Linn. Soc. Lond.*, **169**, 144.

Clark, W. E. Le Gros (1955). *The fossil evidence for human evolution.* Chicago : University of Chicago Press.

Krebs, H. A. & Kornberg, H. L. (1957). Energy transformations in living matter. *Ergeb. phys. biol. Chem.*, **49**, 212.

Mayr, E. (1942). *Systematics and the origin of species.* Columbia University Press.

Mayr, E., Linsley, E. G. & Usinger, R. L. (1953). *Methods and principles of systematic zoology.* McGraw-Hill, New York.

Woodger, J. H. (1945). On biological transformations. In *Growth and form. Essays presented to D'Arcy Thompson* ed. W. E. Le Gros Clark and P. B. Medawar. Oxford : Clarendon Press.

MOULTS AND WINTER WHITENING IN THE MOUNTAIN HARE *LEPUS TIMIDUS SCOTICUS*, HILZHEIMER

BY

RAYMOND HEWSON

Dufftown, Banffshire

[Accepted 12th November 1957]

CONTENTS

	Page
Introduction	99
The summer coat	100
The autumn moult	101
The winter moult	102
The spring moult	104
Factors affecting moulting	105
Summary	107
Acknowledgments	108
References	108

INTRODUCTION

The mountain hare *Lepus timidus scoticus* is one of a group of animals which turn white in winter. Others are the stoat, weasel, collared lemming and ptarmigan, and a number of varying hares (*Lepus* spp.) which are widely distributed in North America, Greenland and northern Europe. The whitest of these hares the Greenland hare, *Lepus timidus groenlandicus*, never becomes brown or grey but in summer " has brownish-grey ears, forehead, crown and occiput and scattered brown and black hairs on the median parts of the back " (Salomonsen, 1939). The brownest of them, the Irish hare *Lepus timidus hibernicus*, whitens very little or becomes merely piebald in winter, although white specimens do occur (Barrett-Hamilton, 1911–13). Indigenous only in the Scottish Highlands the mountain hare has been introduced into south Scotland, the Scottish Islands, and England and Wales. It was originally thought that its white winter coat was due to a loss of pigment from the fur and hair, later that there was a moult to a white pelage. The protagonists on both sides are summarised by, among others, Barrett-Hamilton (1911–1913), Gunn (1932), Lyman (1943), and more fully by Severaid (1945), the last three being chiefly concerned with American varying hares.

It is now established that the white winter coat is due to a moult and it has been shown by Lyman (1943) for the varying hare *Lepus americanus* that the onset of the moult is controlled by a reduction in the amount of light received through the eyes, and conversely that an increase in the length of daily illumination brings about a white to brown moult. Novikov & Blagodatskia (1948) have made similar findings for the varying hare of western Siberia *Lepus timidus sibiricorum*. On the other hand Salomonsen (1939)

has shown for various animals a relation between the degree of winter whitening and mean winter temperature. This will be considered later with regard to the mountain hare. There are three annual moults :

1. A spring moult from white to brown.
2. An autumn moult from brown to brown.
3. A winter moult from brown to white.

The autumn moult appears to have been previously overlooked. Lyman refers to a similar moult in the varying hare as a " preliminary moult " but it appears to correspond to the autumn moult of the brown hare *Lepus europaeus occidentalis* and of the Scottish ptarmigan *Lagopus mutus millaisi*. The winter moult is an additional moult which may be modified by climate as, for example, the incomplete moult of the Scottish ptarmigan compared with the rock ptarmigan *Lagopus m. mutus*, the brown rather than white or piebald coat grown by many English stoats *Mustela erminea*, and the blue-grey winter pelage of the Faroe hare *Lepus timidus seclusus*.

The present work is based on an examination of the skins in the collection of the British Museum (Natural History), a rather casual examination of about 575 mountain hares in autumn and winter pelage at Smithfield Market, London, between 1952 and 1955, a detailed study of 110 skins in my own collection, and observations in the field over periods totalling about three years. Gunn (1932) has shown that the hair root moves towards the outer surface of the skin during growth and Ecke & Kinney (1956) that, as new hair develops, a heavy concentration of pigment is deposited at the follicular site, giving the skin a dark colour. As the hair grows pigment is distributed along the shaft until all pigment is removed from the follicle at full growth. When new pelage growth occurs in the mountain hare, even in the winter moult to a mainly white pelage, the hair root shows as a dark blob on the inside of the skin, indicating clearly where the new hair is appearing although it may be only 1 or 2 mm. long and difficult to locate in the pelage. For this reason I have chiefly used flat air-dried skins. When hair and fur are growing strongly the hair root marks on the flesh side of the skin may coalesce to form continuous patches of colour ; these are known as moult marks and I have kept the term hair root marks for the marks of individual hairs.

Mountain hares in some phase of the moult can be found in every month of the year, and the periods given for the three moults, while including the majority of hares, do not by any means cover them all. The moults of leverets are not considered in this paper.

THE SUMMER COAT

The summer pelage of the mountain hare has three main constituents :

1. The fur, about 15 mm. long at mid-back, grey proximally, brown towards the tip.
2. The pile hair, about 25 mm. long at mid-back, dark grey with a brown sub-terminal band 2 to 4 mm. wide and a black tip.
3. The guard hairs, about 40 mm. long at mid-back, which are black

and project through the pile hair. They are most numerous at the rump. White guard hairs may persist from the winter coat.

In the field the mountain hare appears darker, smokier or bluer than the brown hare or rabbit. The blue colouring is due to long grey fur at flanks, thighs, and rump showing through the pile and guard hairs. The head is a clearer brown than the body and is covered with fur and with short pile hair with brown sub-terminal bands. The whiskers are black, black and white, and white ; there is much individual variation. The ears are dark, almost black, behind and only thinly covered with hair. The nape is grey-brown and woolly, owing to the small number of pile hairs. Variations in the colour of the back from a warm brown overlaying a dark grey-black, to a paler, browner shade, are due to differences in the colour and length of the subterminal bands of the pile hair, which give the pelage its general colour. The underside is grey rather than white, the line of demarcation indistinct, and the whitest fur lies towards the middle line of the ventral surface. Upper surfaces of the front feet are a warm brown (browner than the head if fully moulted) and the pile hair has a wide sub-terminal band and a narrow (1 mm.) black tip. Grange (1932) found twenty-three different colour arrangements in individual summer hairs of the snowshoe hare *Lepus americanus phaenotus* and it is likely that most or all of these can be found in the mountain hare. The ears, upper surface of the tail and the feet may continue to moult throughout the summer pelage and into the autumn moult ; the hind feet rarely become quite brown and even late in June may be almost white.

THE AUTUMN MOULT

The autumn moult begins in June at about the end of the main breeding season. Leverets may be born in July and August, or even later, but sexual chasing diminishes in June and in many male hares the testes are regressing. The earliest moulting skin examined was one of 1st June and the latest was in the earliest stages of the moult on 11th August. No relationship is apparent between moulting and the end of breeding in individual hares. Much of the new fur, pile hair and guard hair is almost the same colour as that it replaces although the sub-terminal bands of the pile hair may be broader and paler. The order of moulting is from the flanks, thighs and shoulders upwards towards the spine, the head last. The fur appears to be replaced in each of the three moults. Lyman (1943) has shown that " although each fur and pile hair is firmly imbedded in its own sheath of epidermal cells, each bunch of hairs goes through a common opening to the exterior, with only an occasional cell separating one hair in the bunch from its fellows ", and that the bases of a fur hair and a pile hair are indistinguishable. Replacement fur can be seen growing in each moult but in the winter moult it is difficult to distinguish in the denser coat.

In the Autumn moult, though a " brown to brown " moult, white guard hairs appear at rump, shoulders and occasionally mid-back (black ones are much more numerous), and white pile hair and fur at the base of the ears and at the hind feet. Some of the skins in the collection of the British Museum

(Natural History) illustrate this (95. 10. 6. 1/2 New Galloway 99. 2. 17. 1 Clonas, 0. 2. 24. 3 Borgie), and others which do not, from Thornhill, Dumfries, more closely resemble the Irish hare which has been introduced into south-west Scotland. The whiskers become white or black-and-white ; cylinders of pigment remaining in otherwise white whiskers suggest that the colour is lost rather than the whiskers replaced. Considerable variation in the progress of the moult among hares of equal size may be due to juveniles from early litters which in August can equal adult measurements but may still be distinguished on handling by the unfused apophysis (Watson & Tyndale-Biscoe, 1953). Two females, killed 10th August, had completed the autumn moult at about the same time as the latest example of the beginning of the moult, but early September skins show new pile hair varying in average length at mid back from 8 to 20 mm., indicating that normally the moult is then in its later stages.

The moult is completed during the second half of September. The mountain hare is then in pelage resembling that of summer ; the hind feet are not yet fully white and the white hairs in the coat are not noticeable in the field. The summer hair and fur are shed before the replacement hair is fully grown.

THE WINTER MOULT

The winter moult begins in the second half of October. It is not obvious in the early phases and there is much individual variation. White guard and pile hairs in the pelage at the beginning of the moult were grown in the autumn moult. The hind feet are whiter than at the end of the autumn moult and moult continuously from July or August until fully white and more densely furred, in the early part of the winter moult. New winter pile hair appears first on thighs and rump and about the same time on shoulders and nape. The growth spreads upwards and along the flanks leaving until last an area of the middle back along the spine, and the head. Towards the end of the moult the ear backs become covered with white fur.

On casual examination the winter pelage appears to contain a fourth type of hair, white and of finer texture than the normal pile or guard hairs. Its base however is indistinguishable from the fur, of which it is therefore a prolongation, reaching at mid-back 25 mm. in length against the 15 mm. of the mass of the fur. Nathan Cohen & Sons Ltd. of Barking, fur processors, who kindly examined several pelage samples, describe this fine white hair as " supporting fibres of the winter pile ". Much of the winter coat however is made up of black pile hair with white or pale buff subterminal bands, similar in length (25 mm.) to that of summer or autumn. The white appearance of the hare (most hares show grey against continuous snow) is due to :

1. " Fine white hair " (fur) projecting as far as or beyond the tips of the pile hair.
2. Pale or white subterminal bands of the pile hair. The way in which the end of the pile hair bends back to form a smooth " backward-pointing " pelage leaves the sub-terminal bands exposed and conceals the dark shafts.
3. White or white-tipped guard hairs.

The pattern of the winter pile hair is apparent when it is only 8–10 mm. long : a black tip 1–2 mm., a white or pale sub-terminal band 4–5 mm. and a dark shaft. Hair root marks remain black throughout the winter moult.

Little of the winter moult is obvious in the field until November. On 10th November 1952 for instance, only one hare in eight examined had a greyish back ; on 17th November 1952 five out of ten hares showed no apparent whitening of the back on gross examination. At that stage the new pile hair, 5–15 mm. long, can only be seen by parting the hair and making a fairly detailed examination. Heavy moult or hair root marks appear in October, and become sparser and less distinct as the new hair lengthens in November. Lyman found that the autumn pile and guard hair was retained in the pelage until the new hair was almost or fully grown, and the fact that hairs with strongly coloured sub-terminal bands persist longest along the spine, the last part of the back to moult, suggests that this is also the case with the mountain hare.

At the end of November hares are mostly in winter rather than autumn or piebald transitional pelage. The forehead is still brown with white extending forward from the base of the ears and upwards from above the nose and cheeks to form a pattern characteristic of this phase of the moult. White fur continues to grow on the ear backs until January. Some coloured hair may remain above the toes on the lower legs, particularly the front legs. If grey or grey-white the back appears to have reached full winter development, remaining autumn pile hairs along the spine being shed as the back finishes moulting in December. The rump is generally whiter and more densely furred than the back. If the back is piebald the winter pile hair and fur will be growing in patches, if grey-brown the new growth will be more even. A hare killed on 9th November, which had been afflicted with a mange-like disease, was growing new white fur and hair at the middle of the nape, ear backs and bases, black fur and hair at the edge of the nape, and brown fur and hair at the forehead.

Severaid (1945) considering moulting in the snowshoe hare *Lepus americanus struthopus* divides the winter moult into seven phases and Salomonsen (1939) considering stoats, weasels and the collared lemming *Dicrostonyx torquatus* as well as varying hares divides it into ten. Such divisions cannot profitably be applied to moults which last so long and vary so much among individuals as do those of the mountain hare. The sequence of change differs from that described by Severaid for the snowshoe hare in that white hairs are grown on the hind feet during the autumn moult, not just after it (Lyman) or during the winter moult (Severaid). Otherwise the order of moulting appears to be the same. Salomonsen shows a phase WB appropriate to the mountain hare at the beginning of the winter moult, that is, white hairs growing on legs only, no winter hairs growing ; and the sequence described by him for the winter whitening mammals mentioned earlier is appropriate to the mountain hare. None of these authors mentions the growth of white hair during the autumn moult.

The final moulting phases are completed slowly. In mid-December 1952 only two out of fifty-four hares examined had patchy or piebald coats ; on

14th December 1956 only one out of thirty-five. Although the growth of winter hair on the body usually finishes about mid-December, hair may be growing strongly on the head, or in some cases the head may still be brown and free of hair root marks indicating that it has still to moult or that it will not moult during the winter. On the body then the moult finishes from the middle to the end of December ; on the head not until late January or early February. When the winter growth is completed the head appears noticeably rounder owing to the longer denser fur and hair. Throughout the pelage the fur is longer, denser, and of finer texture than in summer or autumn. Some brown may persist above the toes ; of fourteen hares chosen at random from sixty-three examined on 2nd February 1955 four showed some colour above the toes.

As a guide to the final phases of the moult hares examined in December and January were divided into those with white or grey-white heads and those with brown heads.

TABLE 1

Locality	Date	Number examined	Mainly grey or white heads	Percentage
Banffshire	14 Dec. 56	35	7	20
* Nairn	15 Dec. 52	33	16	48
* Perthshire	30 Dec. 54	16	10	63
* Inverness-shire	11 Jan. 55	71	28	40
* Perth-shire	11 Jan. 55	48	26	54
Banffshire	12 Jan. 57	71	48	68
* Perthshire	2 Feb. 55	46	38	83
Banffshire	9 Feb. 57	147	123	84
* Perth-shire	16 Feb. 55	16	15	94
* Nairn	23 Feb. 53	10	9	90
* Nairn	2 Mar. 53	22	19	86

* At Smithfield Market, London. Shot several days earlier.

Compared with varying hares from more northerly regions the mountain hare takes longer over the moult and retains its full winter coat for a shorter time. The Greenland hare is in winter coat from August to May and *Lepus timidus timidus* of Scandinavia is white from October to June (Salomonsen, 1939). The snowshoe hare of North America is in winter coat only from January to March (Severaid, 1945) and with a winter moulting period of eleven weeks does not differ greatly from the mountain hare although the mean January temperature may be 7° C. less. *Lepus timidus varronis* of the French Alps may be in winter pelage from early December to April but there is much variation with altitude (Couturier, 1955).

THE SPRING MOULT

The spring moult begins in February and March, and the breeding season at about the same time. A large proportion of male hares have the testes fully grown and descended in early February, rather earlier than the beginning

of the the moult, and of females examined on 13th February 1956 ten out of thirty-one contained young. In the field the new brown hair may not show until late March or early April. The order of moulting is roughly the reverse of the winter moult ; the head first then the upper back, thighs and shoulders, and rump, and finally—much later—the feet.

Heavy hair root marks on the skin of the back, indicating a strong growth of new hair, rarely occur before the beginning of March when the new pile hair is only 5–10 mm. long. Later in the month the first summer hairs become long enough to appear as small brown patches on an otherwise mainly white hare, but these patches are generally not distinct until April. Fur and winter hair are lost before the new coat is grown, sometimes leaving bald rather scaly patches, or the shed white fur may hang loosely in the coat. Growth of new pelage appears less even and regular than in the other two moults and hares are often piebald and ragged looking.

During May hair root marks become indistinct as the new pile hair is approaching its full length, and the head is generally brown. But loose white fur in the pelage suggests that the moult is less advanced than it really is. No skin examined in May was free of hair root marks, and white hair on the hind feet persists into June, and to some extent, throughout the summer. The gap between the end of the spring and the beginning of the autumn moult is therefore very short—certainly less than a month, possibly only a week or two.

FACTORS AFFECTING MOULTING

Two factors may be concerned in the growth of a white winter pelage, a reduction in daily illumination, and temperature. Lyman (1943) has shown that a reduction in the amount of light received through the eyes will bring on a moult to white winter pelage regardless of temperature. It might be of interest to note here that in 1809 Bingley referred to mountain hares kept in "stoved apartments" which still turned white in winter. Yet the Faroe hare *Lepus timidus seclusus* introduced from Norway in 1854–5, had ceased to turn white in winter by 1900 (Williamson, 1948), although a third moult, to a blue-grey winter pelage, may still occur. An increase of about 7° C. in February mean monthly temperature appears to have been sufficient in this case to suppress or alter the character of the winter moult. It has been suggested that mountain hares introduced into the Peak area would cease to whiten in winter, but skins from Derwent, Derbyshire, show no appreciable difference from Scottish Highland skins of the same period. As the difference in February mean monthly temperatures between Buxton and Braemar, at similar altitudes, is only 1–2° C. no change caused by a rise in mean winter temperature can be expected. The typical habitat of the mountain hare in northern Scotland is moorland from 1000–2500 ft. and the Pennine hares live at a similar altitude. A slightly greater variation in temperature occurs between north-east and south-west Scotland and winter skins from Selkirkshire can be picked out by their browner colouring caused by the absence of the "fine white hair" which usually masks the colour remaining in the pile hair. Nathan Cohen and Sons Ltd. found that the south Scotland pelage

was less dense and of coarser texture. The difference is not at all clearly marked and not enough material has been examined to test its significance.

A greater variation in temperature occurs between grouse moors at 1000–1500 feet and the high Cairngorm plateaux at 3000–4000 feet, and Smith (cited by Bourlière, 1955, p. 122 but reference not given) has described differences in the progress of the moult in American varying hares at altitudes of 2800, 3200 and 4000 feet respectively. More striking differences are to be found in the varying hare of the French Alps which has a very wide altitudinal range, probably from about 4000 to over 8000 feet. Couturier found that a captive male from a sub-Alpine district had almost finished the spring moult on 8th April when another, from a high altitude, had barely started it. Alpine hares kept in captivity at Grenoble, 700 feet, had the winter moult retarded and the spring moult brought forward. They never became as white as the wild hares of the region. Unfortunately no similar comparison can be made here, because what few hares there are in the high Cairngorms can within their normal range descend 1000 feet, or more, and the amount of individual variation exhibited among so few hares would rule out reliable results. It does seem however that the progress of the spring moult may vary in the same area in different years. On Carn na Larach, Slochd, Inverness-shire, on 22nd May 1951, four feet of snow remained in drifts in birch woods on the lower slopes of the hill, after a severe winter with heavy snow. Of twenty-eight mountain hares seen about fourteen showed loose white fur and hair in the pelage. On 23rd May 1956, after a milder winter and spring, only eight out of thirty-six hares showed loose winter fur ; and six skins obtained in Banffshire, Moray, and Derbyshire between 9th and 20 May 1956 showed no loose winter fur at all.

Rothschild (1942) has shown that a marked fall in temperature greatly accelerates the winter moult of stoats *Mustela erminea*, and states also that a limited blanching of guard hairs occurs before they are shed. The following factors suggest that some blanching may occur in the pelage of the mountain hare :

1. The presence in pale, almost white subterminal bands of the pile hair, of blobs or cylinders of brown pigment, found in only a few hairs among others with uniformly pale sub-terminal bands.
2. The whiskers, mainly black in summer, are white or black-and-white in autumn and winter. In the white or grey tips of the whiskers similar blobs of colour may be found.
3. November pile hair often has narrower more strongly coloured sub-terminal bands than that of January.

Nathan Cohen & Sons Ltd. found evidence of blanching in the sub-terminal bands of the winter pile hair and tips of the guard hair, but gave no details. Rothschild also found in captive stoats a marked individual variation in moulting even between animals from the same litter, which among them under the same conditions displayed no colour change, a partial colour change, a complete colour change, and a complete colour change repeated in subsequent winters without renewed exposure to cold. This same " genetic factor "—individual variation—may perhaps occur in mountain hares also but a study of captive animals is necessary to establish this.

In time of year and duration the moults of the mountain hare resemble those of the Scottish ptarmigan. Although the seasonal pattern of weather is the same for both it should be borne in mind that the ptarmigan, at 3000 feet, lives in an environment 3° C. or more colder than the mountain hare which lives mainly at about 1500 feet.

The threshold temperature of −4·5° C. (mean of the coldest winter months) given by Salomonsen for the appearance of a pigmented winter coat in *Lepus timidus* is too low for the mountain hare which moults to a mainly white pelage at a temperature (mean of coldest winter months) of −1° to 1° C. at an altitude of 1000–1500 feet.

TABLE 2

	Autumn	Winter	Spring
Mountain hare	early June–mid Sept.	mid Oct.–early Feb.	mid Feb.–end May
Scottish ptarmigan	end June–mid Sept.	end Sept.–early Feb.	mid Feb.–early May

Dates of Scottish ptarmigan moults from Salomonsen (1939) except the spring moult which is from Dr Adam Watson's unpublished thesis on ptarmigan.

SUMMARY

1. The mountain hare undergoes three annual moults. These are a spring moult from white to brown, an autumn moult from brown to brown, a winter moult from brown to white.

2. Flat air-dried skins were used to trace the course of the moults because new growth is clearly indicated by hair root marks on the flesh side of the skin.

3. The pelage of the mountain hare consists of fur, pile hair and guard hair. The summer pelage is described.

4. The autumn moult begins in June and ends in September. It begins about the end of the main breeding season. Some white hair is grown, particularly on the feet.

5. The winter moult begins in October. Winter fur is longer, finer in texture and denser than that of summer or autumn. Projecting as "fine white hair" to the tips of the pile hair it is largely responsible for the hare's white colouring. Moulting on the body ceases in December; on the head not until January or early February.

6. The spring moult begins in February, rather later than the beginning of the breeding season. Pelage is shed before replacement in this moult and in the autumn moult; in the winter moult the old hair is only shed when the new hair is almost or fully grown.

7. No significant regional variations, owing to temperature, occur within England and Scotland. Variations in the progress of the moult, due to temperature, may occur.

8. There is some blanching of winter pile and guard hairs and probably of whiskers.

9. In season and duration the moults resemble those of the Scottish ptarmigan.

ACKNOWLEDGMENTS

For help in connection with this paper I am indebted to A. S. Juniper Ltd. for permission to examine mountain hares in their premises at the London Central Market at Smithfield, and to their game department staff for help during such examinations ; to Nathan Cohen & Sons Ltd., fur processors, of Barking, particularly Mr W. Durber, for examining skins ; to various game-keepers for sending skins ; to Mr H. N. Southern for reading the draft of this paper, and to Dr Adam Watson for reading the draft and allowing me to use material from his unpublished work on ptarmigan.

REFERENCES

Barrett-Hamilton, G. E. H. (1911–1913). *A history of British mammals.* London : Gurney and Jackson.

Bingley, W. (1809). *Memoirs of British quadrupeds.* London : Darton, Harvey & Darton.

Bourlière, F. (1955). *The natural history of mammals.* London : Harrap.

Couturier, M. (1955). Le pelage du Lièvre variable des Alpes *Lepus timidus varronis. Terre et Vie* **2,** 101–116.

Ecke, D. H. & Kinney, A. R. (1956). Aging meadow mice *Microtus californicus* by observation of moult progression. *J. Mammal.* **37,** 249–254.

Grange, W. B. (1932). The pelages and color changes of the snowshoe hare *Lepus americanus phaenotus. J. Mammal.* **13,** 99–116.

Gunn, C. K. (1932). Color and primeness in variable mammals. *Amer. Nat.* **66,** 546–559.

H.M. Stationery Office. *Averages of temperature for Great Britain and Northern Ireland* 1921–50. London.

Lyman, C. P. (1943). Control of coat color in the varying hare *Lepus americanus* Erxleben. *Bull. Mus. comp. Zoöl. Harvard* **93,** 391–461.

Novikov, B. G. & Blagodatskia, G. I. (1948). Mechanism of development of protective seasonal colorations. *Dokl. Akad. Nauk. SSSR.* **61,** 577–80 cited by Couturier above.

Rothschild, M. (1942). Change of pelage in the stoat *Mustela erminea* L. *Nature, Lond.* **149,** 78.

Salomonsen, F. (1939). Moults and sequence of plumages in the rock ptarmigan (*Lagopus mutus* (Montin)). *Vidensk. Medd. Dansk Naturh. Foren.* **103,** 1–491.

Severaid, J. H. S. (1945). Pelage changes in the snowshoe hare (*Lepus americanus struthopus* Bangs). *J. Mammal.* **26,** 41–63.

Tyndale-Biscoe, C. H. & Watson, J. S. (1953). The apophyseal line as an age indicator for the wild rabbit *Oryctolagus cuniculus. N.Z.J. Sci. Tech.* (B) **34,** 427–435.

Williamson, K. (1948). *The Atlantic Islands.* London : Collins.

THE DISTRIBUTION OF THE BARNACLE *ELMINIUS MODESTUS* DARWIN IN FRANCE

BY

M. W. H. BISHOP

National Institute for Medical Research, London, N.W.7.

AND

D. J. CRISP

Marine Biology Station, University College of North Wales, Menai Bridge, Anglesey

[Accepted 12th November 1957]

(With 2 figures in the text)

CONTENTS

	Page
Introduction	109
Present distribution	111
Environmental influences	113
History	115
Acknowledgments	117
Summary	118
References	118
Appendix of records	120

INTRODUCTION

The Australasian barnacle *Elminius modestus* Darwin had successfully colonised the Portsmouth area on the south coast of England at least as early as 1944 (Stubbings, 1950), although it was not noticed until 1945 when Bishop (1947) first demonstrated its presence in Chichester Harbour. Its discovery also in the river Crouch on the south east coast in 1945, in Plymouth in 1946 (Crisp, 1948), in the Falmouth area (Knight-Jones, 1948) and in South Wales in 1947 (Crisp & Chipperfield, 1948) indicated that it had probably been established for several years. It is now (1956) common in the estuaries of southern England, and, with the exception of Lyme Bay, along most of the south coast. (See Fig. 1).

Records from the mainland of Europe have hitherto been scanty except for those from the Dutch coast, which have been summarised by den Hartog (1953). *Elminius* was first noticed in the Kijkduin district in Southern Holland (Meulen, 1946), and its presence subsequently reported by Boschma (1948). Den Hartog (1953) has described its northward spread from the Hook of Holland ; it reached the Zuider Zee by 1950, the northernmost Friesian islands by 1951, and, according to Kühl (1954), arrived at Cuxhaven in 1953. Thus it covered 20–30 kilometres during the first two years, and thereafter spread at a steadily increasing rate covering 50–70 kilometres a year.

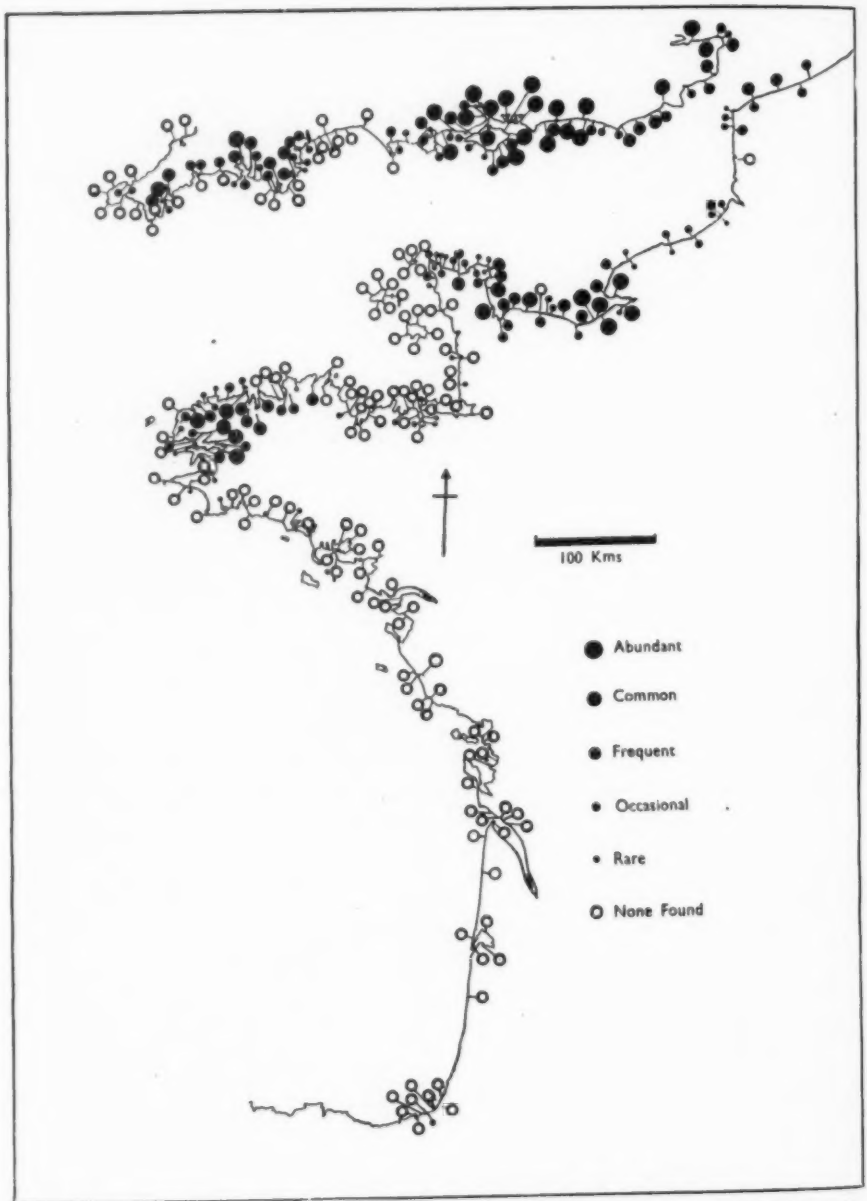


Fig. 1.—The distribution of *Elminius modestus* on the coast of France, based on records observed between 1953 and 1955, and on the south coast of England from records observed between 1950 and 1956. The records are classified into six categories of abundance, details of which are given in the Appendix. Records from ports or other enclosed areas, and from river estuaries are shown to the landward side of the coastline, records from the open coast are shown on the seaward side.

According to den Hartog, *Elminius modestus* spread southwards from the Hook of Holland across Belgium and France. He has suggested that it extended its range from the Isle of Schouwen to at least as far as Wimereux, a distance of 200 kilometres or more, between 1948 and 1950. But when Bishop (1954) discovered it at Wimereux in 1950 it was already present in large numbers, so that if it were advancing southwards the boundary must have been further along the coast at that time. Leloup and Lefèvre (1952) recorded *Elminius* on a Belgian Fishery Research vessel in 1950, on *Portunus holsatus* off Ostend in 1952, and in the Ostend-Bruges canal during the same year. They also make the important observation that they had searched for it in vain on the Belgian coast in 1946 and 1947.

Bishop (1954) has described the distribution of *Elminius* in north-west France in 1953. He showed that another independent centre of dissemination must be postulated, probably in the Rade de Brest, since the species was found throughout the west and north of the Brittany peninsula, but was absent from the Gulf of St. Malo to the east.

In 1954 and also in 1955 (M.W.H.B.) we investigated in much greater detail the occurrence of *Elminius* along the whole of the Channel and Atlantic coasts of France. The object of this survey was to define the distribution of this immigrant species on the French coast in order to provide a basis on which further extensions of its range could be established. At the same time we hoped that the results might suggest the course of events which have led to the present distribution.

PRESENT DISTRIBUTION

Our detailed records are summarised in the Appendix, which includes for completeness other published observations from the coasts of the European mainland. Fig. 1 illustrates the distribution of *Elminius* in France in 1953 and 1954, and shows not only its abundance where it occurred, but also the places from which it was apparently absent, a long search having failed to reveal it. Where the coast was clearly unsuitable for barnacles no indication of presence or absence is shown. The figure includes observations on the south coast of England made between 1950 and 1956, details of which will be published separately. The quantitative classification is based on examination and counts made on suitable surfaces ; in many instances we have made records in the same area independently and these observations usually agreed closely wherever the barnacle was present in measurable abundance. Where the barnacle was present in small numbers and found by one of us only, a positive record is shown.

Our observations show that the incidence of *Elminius* falls into four sectors. The first extends from Belgium to Cap de la Hague. Throughout this region the distribution of *Elminius* is practically continuous, and its abundance appears to be related mainly to the type of shore. It covers a fair proportion of the available surfaces found along the predominantly sandy stretches of this coast, as for example the dune coast to the east of Calais, while it is especially abundant in the region between Le Havre and St. Vaast la Hougue. These sandy stretches are rarely exposed to heavy swell. By contrast it is

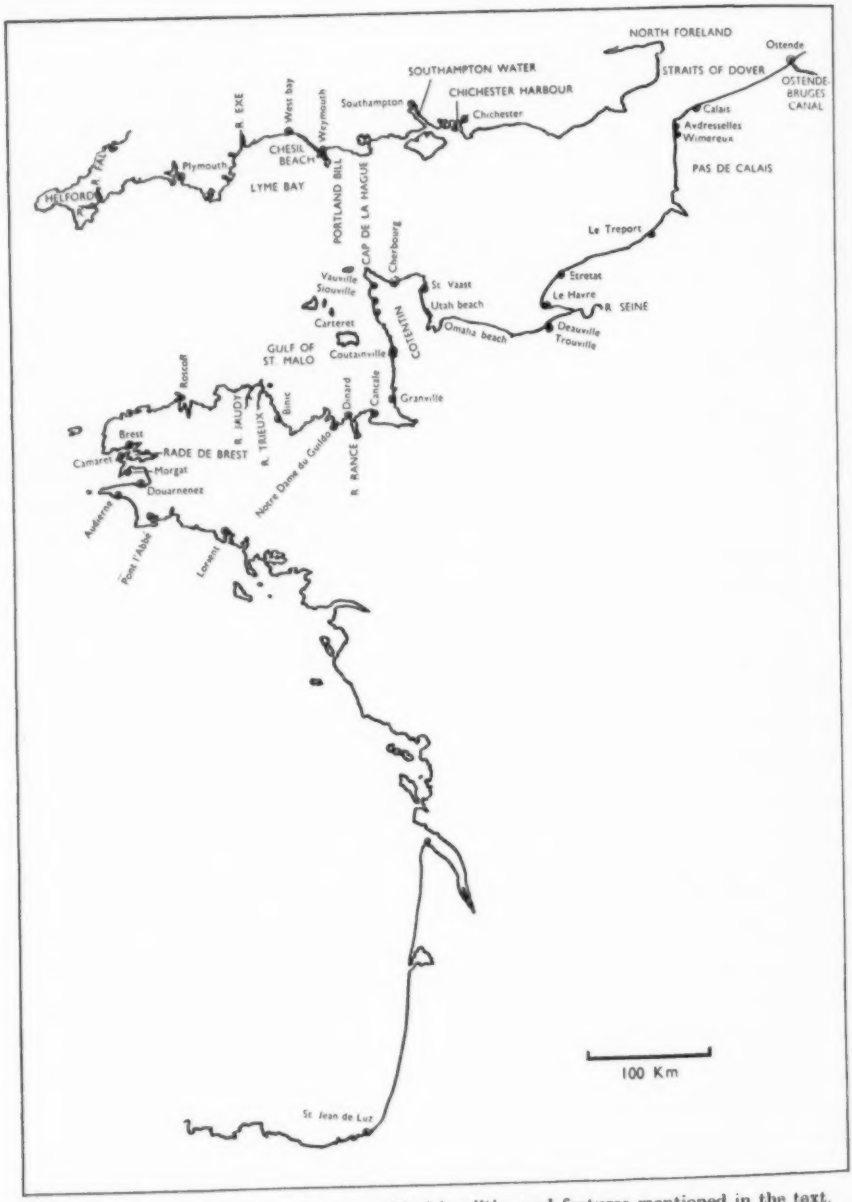


Fig. 2.—Map showing the main geographical localities and features mentioned in the text.

rather sparse on the chalk between Etretat and Le Tréport, and at Cap Blanc Nez, and scarcely more common at Wimereux and Audresselles despite the existence there of plenty of firm rock surfaces. These last mentioned localities face west, and are perhaps too exposed to waves to provide very suitable habitats for *Elminius*. Nevertheless, it is found in surprising regularity along the whole of the north coast of the Cherbourg peninsula as far as Cap de la Hague, not only in the shelter of Cherbourg harbour, but also on quite exposed rocky promontories. Throughout this sector, excepting only the north of Cotentin, *Elminius* occurs in about the same abundance on the open shoreline as in harbours and estuaries. This may reflect the shelter afforded to the intertidal zone by the gently shelving character of the beaches, which cause the waves to lose much of their force far out to sea.

In the second sector, which runs from Cap de la Hague to the estuary of the Trieux, the incidence of *Elminius* is negligible. A few specimens were found along the west coast of Cotentin at Vauville, Siouville, Coutainville and Granville, a small number in the estuary of the Rance, and single specimens at Notre Dame-du-Guildo and Binic. Much of this coast offers apparently suitable habitats for the species to gain a hold. Most notable among these is the valley of the Rance. Nevertheless very thorough examinations in 1953, 1954 and in 1955, failed to reveal any increase in the population.

The third sector stretches from the estuary of the Jaudy to the Rade de Brest. Here *Elminius* is plentiful in all the major estuaries. Its distribution in this sector differs from that of the eastern part of the Channel coast in the restriction of the species to estuaries and harbours, few specimens being found outside on the open rocky coasts.

The last sector stretching south from the Rade de Brest is but thinly populated. Isolated specimens were found at Camaret, Morgat, Douarnenez, Audierne, Pont-l'Abbé, Lorient and St. Jean-de-Luz, but nowhere were the numbers sufficient to form an expanding population, although many suitably sheltered areas exist. The specimen taken at St. Jean-de-Luz is worthy of special mention, on account of its great distance from all other centres of population.

If the distribution on the coast of France is compared with that of the south coast of England (Fig. 1), a striking similarity is apparent. Three similar sectors are found approximately opposite to the corresponding sectors on the French side. The first, in which *Elminius* occurs abundantly both in harbours, estuaries and on many parts of the open coast, runs from the North Foreland to Weymouth. The second sector with a sparse population of *Elminius* is restricted to Lyme Bay, between Portland Bill and the Exe. The third sector, where *Elminius* is confined mainly to estuaries, stretches westwards from the Exe. Plymouth Sound and the Fal and Helford Rivers are the main centres of dissemination in this area.

ENVIRONMENTAL INFLUENCES

There can be little doubt that the correspondence between the three sectors of distribution of *Elminius* is a result mainly of the similarity in environmental conditions on the north and south coasts of the English Channel.

In the east, the rocks of both coasts are mainly soft and friable. They have formed a shoreline of smooth contour, large stretches of which are covered with beach material as a veneer of sand and shingle on a gently shelving wave cut platform (see Johnson, 1919). These conditions appear to favour *Elminius*, so long as there are surfaces available for settlement well above the abrasion level, such as piers, breakwaters, jetties, groynes or harbour works.

In the west, Brittany and the south western peninsula of England offer similar sheltered habitats in the form of drowned valleys, outside which the coast is wave beaten and unfavourable.

The scarcity of the species in Lyme Bay and in the Gulf of St. Malo cannot, however, be explained entirely by the similarity of the environment. Lyme Bay has a few rocky areas towards its western end but contains much shingle. This has accumulated at the east end of the bay to form a bank of shingle fifteen miles long known as Chesil Beach. There are few habitats suitable for *Elminius* other than the small enclosed harbour of West Bay. Although the east side of the Gulf of St. Malo is rather unfavourable for *Elminius* on account of accumulated sand, gravel and shingle, it cannot be compared with Chesil Beach, for there are many local habitats apparently suitable for the species and many rocky areas supporting a good fauna (e.g. at Carteret). The rest of the Gulf, west of Cancale, is well suited to barnacle settlement and possesses many harbours and estuaries. Thus while the scarcity of *Elminius* in Lyme Bay may be attributable to the obvious lack of suitable habitats, a different reason must be put forward to account for its absence from much of the Gulf of St. Malo.

Since *Elminius* is an immigrant species which is still extending its range, there are two possible explanations for regions of scarcity. The first is that the environment is intrinsically so unsuitable that the species could never become abundant. The second is that, though the area may be suitable, *Elminius* is slow to reach it, or is slow to form a stable population. It is obvious that an immigrant species will flourish best and colonise most rapidly where the environment is most suitable for its reproduction, and where the larvae are retained in a small body of water. These conditions are fulfilled on both north and south coasts at the eastern end of the Channel since these shores provide suitable habitats and have high summer temperatures which encourage breeding (Crisp & Davies, 1955). Moreover, in partially enclosed areas such as Southampton Water, the Thames estuary, the Essex rivers, and the Seine estuary, tidal movements carry the same body of water to and fro with relatively small larval losses offshore. These form ideal centres of propagation.

The coastlines of Brittany and south-western England offer more restricted habitats because *Elminius* is not suited to live on exposed coasts. Within the upper reaches of the drowned valleys, however, there is both shelter and water retention, thus providing suitable areas in which isolated populations may develop.

A coastline such as that of Lyme Bay, east of the Exe, offers neither shelter nor appreciable retention of water, while, at the eastern end, Chesil Beach forms a barrier to the spread of any intertidal species. The tidal races off Portland Bill will tend to carry larvae from Weymouth far afield and so prevent

high local population densities existing in Lyme Bay. It is not surprising therefore that this is the only part of the south coast of England on which *Elminius* has not yet become established, and it is unlikely that it will ever become abundant there except possibly in the inner harbour of West Bay.

The eastern side of the Gulf of St. Malo resembles Lyme Bay in having strong tidal currents and in its lack of large bodies of sheltered water. This no doubt has offered a barrier to the westward spread of *Elminius* from Cap de la Hague. Between Cancale and the Trieux, however, conditions would appear to be suitable for the species, so that the absence of *Elminius* from this stretch of coast and the colonisation first of the Brest and Roscoff areas to the west might be a mere historical accident. There is, however, an alternative explanation of the scarcity of *Elminius* in the Gulf of St. Malo.

In colonising an indented rocky coastline, *Elminius* must depend first on the establishment of local populations in enclosed areas, notably at the heads of bays and estuaries. Some larvae are inevitably swept out to sea by the tides and are then dispersed over so wide an area that they may not settle close enough to breed (Crisp, 1950). If sufficient remain and settle in the estuary, a population density high enough for successful breeding can be attained and the population will expand and eventually cover some of the coastline outside the estuary itself. The abundance of *Elminius* in the Jaudy and its absence from the neighbouring estuary of the Trieux indicate how local are the initial population centres on such a coast.

The Gulf of St. Malo has exceptionally large tides (Doodson & Warburg, 1946) reaching 12 metres at Equinoctal Springs at Cancale (Admiralty Tide Tables, 1956). These must cause a greater exchange of estuarine water with the sea than those which occur in estuaries on the opposite side of the Channel, or in estuaries lying to the east or west, where the tidal range is smaller. Therefore the initiation of a stock of *Elminius* in an estuary such as the Rance will be more difficult than elsewhere. The facts obtained to date support this explanation, for small numbers of individuals which have been found at scattered points in the Rance indicate that the species has been introduced, but nowhere has it reached sufficient abundance to produce an expanding population. Moreover, there was no appreciable increase in the population between 1953 and 1955, though as early as March 1952 Dr M. Franc (see den Hartog, 1956) recorded *Elminius* larvae near Dinard. Probably exceptionally favourable circumstances must occur before the species is able to take hold in such an estuary.

HISTORY

The great distance separating the two main populations in France suggests that the colonisation of Brittany and that of the coastline east of Cherbourg must have taken place independently. There is no evidence to indicate which occurred first, and neither population shows at present any appreciable tendency to extend its range or to increase in its abundance. The earliest record for the Roscoff area, that of Dr P. Drach in 1952 (personal communi-

cation), was later than the earliest record at Wimereux where the species was common in 1950 (Bishop, 1954). This suggests that the eastern population may have been established before the western. The Brittany population probably originated from Brest and was carried to neighbouring estuaries on the Channel coast by shipping, and perhaps by larvae transported by the residual current that is believed to flow northward round the peninsula (Warburg, 1945). The absence of any appreciable settlements south of Brest is surprising, since coastal traffic in this direction is considerable and there are many estuarine habitats that appear satisfactory. There is, unfortunately, little reliable information on the direction of residual currents in the northern part of the bay of Biscay (Warburg, 1945).

The origin of the population of the eastern sector of the French coast is even more obscure. The Seine estuary, including the Le Havre and the Deauville-Trouville areas, is probably the most favourable for the development of an initial population, though Cherbourg harbour is an alternative or additional possibility. The Normandy coast, where many ships from Britain were sunk during the Allied invasion in 1944, is a likely source, as suggested by den Hartog (1956), but in the immediate vicinity of the invasion beaches the shores are open to storms and offer few suitable surfaces for settlement. More probably, larvae may have been carried thence by westerly drifts into the Seine area or have been brought directly by shipping using Le Havre soon after the invasion. It is unlikely that the species could have reached the French coast before 1944, since there was virtually no sea communication between Britain and France between 1940 and 1944.

The population of *Elminius* in Northern France now appears as stable and well established as that on the British side, which suggests, by analogy with its rate of spread in Britain, that it has existed for at least seven to ten years. This period is comparable with the time during which *Elminius* has been known in Holland. The populations in Holland and in France are now continuous; their possible origins should therefore be considered together.

The first individuals were found in Holland in 1946 when, according to den Hartog (personal communication), "*Elminius* was observed in great quantities on drifting objects washed ashore along the whole Dutch coast". It has hitherto been assumed that the species was transported to Holland by shipping from East Anglia, largely because the earliest records were made near the Hook of Holland and Rotterdam, and also because as early as 1946 the species was observed on a ship which had plied between Harwich and the Hook of Holland (Bishop, 1947). But even early in 1947, according to den Hartog, although all regular observers and collectors had been warned, there were few records other than those from drifting objects. This drifting material travels from west to east along the dune coasts of Belgium and Holland. Since these objects sometimes bear barnacles, such as *Balanus perforatus*, (den Hartog, 1953) which are found only in the western part of the Channel, it is reasonable to suppose that they are transported by the main residual flow which is known to pass through the Straits of Dover from west to east (Carruthers, 1930). Minor counter-currents on either side of the main drift through the Straits have been observed by Van Veen (1936)

but it is doubtful whether these would greatly assist any spread from east to west. It follows, therefore, that while *Elminius* might conceivably have spread from France, or even from England, into Holland, any spread in the opposite direction is improbable and would have been extremely slow. Further, since the dissemination of intertidal animals across sea barriers does not appear to happen very easily (Crisp & Southward, 1953) and since both sides of the Straits of Dover are somewhat sparsely populated by *Elminius*, it is unlikedly that the species spread directly from British coastal waters to the Continent. Hence two possibilities are left ; either there were two separate immigrations, one to the French coast and the other to the Dutch coast, or alternatively a single immigration to the French coast followed by an eastwards spread into Holland.

den Hartog (1953) believed that *Elminius* spread both northwards and southwards from a centre near the Hook of Holland. His map indicating the annual changes in the population of *Elminius*, while showing clearly the northward spread, does not convincingly demonstrate any spread to the south. Moreover, he himself commented on the fact that the southwards migration into the Pas de Calais appeared to be faster than the northwards migration, despite the fact that the main current would favour the latter.

The specimens recorded from the Pas de Calais in 1950, however, can now be considered as part of the French population spreading from the west, which by this time had become continuous with the Dutch population. Could this eastward spread have occurred sufficiently rapidly to have given rise to the centre established in Holland between 1946 and 1947 ? den Hartog's records for Zeeland appear to be consistent with a general increase having occurred over the whole area between 1946 and 1948 with populations expanding into the channels of the Rhine, such as might have been expected if a rapid extension of the species had taken place along the whole Dutch coast. The many records from floating objects are consistent with the view that these populations originated from France. There are however two arguments against this conjecture. First, the rate of spread of *Elminius* from Le Havre to the Rhine would have been 200 kilometres a year if it first reached France in 1944 and Holland in 1946. Secondly, Leloup and Lefèvre (1952) were unable to find *Elminius* on the Belgian coast in 1946 or 1947. It is therefore probable that the populations in France and Holland were at that time separate, and therefore had independent origins. The population on the French coast probably spread eastward, meeting the Dutch population along the Belgian coast in about 1949 or 1950.

According to Kühl (1954), the population of *Elminius* in Cuxhaven also began as an isolated centre, but there are insufficient records available on the North German coast to indicate clearly its status in this area.

ACKNOWLEDGMENTS

We are indebted to the Royal Society for a grant from the Browne Fund to enable one of us (M.W.H.B.) to carry out the survey in 1954. We wish to thank Dr A. J. Southward for generously making available to us his records for the Channel Islands.

SUMMARY

1. The distribution of *Elminius modestus* along the coast of France may be divided into four sectors. From the Belgian frontier to Cap de la Hague, it is ubiquitous both on the coast and in harbours wherever suitable surfaces for settlement exist. From Cap de la Hague to the Trieux estuary, it is scarce or absent. From the Jaudy to the Rade de Brest, it is plentiful in all sheltered estuaries but scarce on the open coast. South of the Rade de Brest, only isolated individuals have been met in a few estuaries, the furthest afield being at St. Jean-de-Luz close to the Spanish frontier.

2. The distribution on the Channel coast of France resembles closely that on the coast of southern England.

3. It is suggested that the tidal races and the absence of large bodies of sheltered water form a barrier to its westward spread both at Portland Bill and at Cap de la Hague.

4. Conditions in the Gulf of St. Malo, unlike those in Lyme Bay, are probably not directly unfavourable to the growth and development of individuals, but are probably unfavourable for the initial establishment of a population on account of the large tides that occur there. These may sweep locally developing populations of larvae out of the river systems and so disperse them too widely for reproduction to be possible.

5. The Brittany population and that of the eastern part of the Channel must have been established independently. Both are now fairly stable and well established.

6. The Brittany population is most likely to have been disseminated from the Rade de Brest ; that east of Cap de la Hague either from Cherbourg or more likely from Le Havre, Trouville and the Seine estuary, perhaps at or soon after the Allied invasion in 1944.

7. The populations in Holland and France, though now continuous, probably arose independently. The two populations probably merged on the coast of Belgium approximately in 1949–1950.

REFERENCES

Admiralty Tide Tables (1956). London. Hydrographic Dept., Admiralty.

Bishop, M. W. H. (1947). Establishment of an immigrant barnacle in British waters. *Nature, Lond.* **159,** 501.

Bishop, M. W. H. (1954). *Elminius modestus* in France. *Nature, Lond.* **173,** 1145.

Boschma, H. (1948). *Elminius modestus* in the Netherlands. *Nature, Lond.* **161,** 403–404.

Carruthers, J. N. (1930). Further investigations upon the water movements in the English Channel. Drift bottle experiments in the summers of 1927, 1928 and 1929, with critical notes on drift bottle experiments in general. *J. Mar. biol. Ass. U.K.* **17,** 241–275.

Crisp, D. J. (1948). *Discovery,* p. 229.

Crisp, D. J. & Chipperfield, P. N. J. (1948). Occurrence of *Elminius modestus* Darwin in British waters. *Nature, Lond.* **161,** 64.

Crisp, D. J. (1950). Breeding and distribution of *Chthamalus stellatus*. *Nature, Lond.* **166,** 311.

Crisp, D. J. & Southward, A. J. (1953). Isolation of intertidal animals by sea barriers. *Nature, Lond.* **172,** 208.

Crisp, D. J. & Davies, P. A. (1955). Observations *in vivo* on the breeding of *Elminius modestus* grown on glass slides. *J. Mar. biol. Ass. U.K.* **34,** 357–380.

DEN HARTOG, C. (1953). Immigration, dissemination, and ecology of *Elminius modestus* Darwin in the North Sea, especially along the Dutch coast. *Beaufortia* **4,** 9–20.

DEN HARTOG, C. (1956). Speculations on the immigration of the barnacle *Elminius modestus* in France. *Beaufortia* **5,** 141–142.

DOODSON, A. T. & WARBURG, H. D. (1946). *Admiralty manual of tides.* London: H.M. Stationery Office.

JOHNSON, D. W. (1919). *Shore processes and shoreline development.* New York: John Wiley & Sons.

KNIGHT-JONES, E. W. (1948). *Elminius modestus*: Another imported pest of East Coast oyster beds. *Nature, Lond.* **161,** 201.

KÜHL, H. VON (1954). Uber des Aufreten von *Elminius modestus* Darwin in der Elbmundung. *Helgöland wiss. Meeresunters.* **5,** 53–56.

LELOUP, E. & LEFÈVRE, S. (1952). Sur la présence dans les eaux de la côte belge du Cirripède, *Elminius modestus* Darwin etc. *Bull. Inst. Roy. Sci. nat. Belg.* **28,** No. 48, 1–6.

MEULEN, H. VAN DER (1946). *Het. Zeepaard,* 7, Nos. 6–7.

STUBBINGS, H. G. (1950). Earlier records of *Elminius modestus* Darwin in British waters. *Nature, Lond.* **166,** 277–278.

VAN VEEN. (1936). *Onderzoekingen in de Hoofden in verband met de Gestelheid der Nederlandsche Kust.* 's Gravenhage.

WARBURG, H. D. (1945). *Tidal streams of the waters surrounding the British Islands and off the west and north coasts of Europe.* 2nd Ed. London: Hydrographic Dept., Admiralty.

APPENDIX OF RECORDS [see overleaf]

APPENDIX OF RECORDS

Records of *Elminius modestus* Darwin on the European mainland. Key to frequency ratings :—

A. Abundant. 30 per cent or more of available surfaces well covered. Adults one per sq. cm. or more frequent.
C. Common. Covering less than 30 per cent of available surface but most individuals within 1–2 cms. of each other. Frequency 0·1–1·0 per sq. cm.
F. Frequent. Readily found, about half the population distributed within 3 cms. of each other and so able to breed. Spat not usually plentiful. Population density of adults 0·01–0·1 per sq. cm.
O. Occasional. Very local and must be searched for. Majority isolated. Population density 1–100 per sq. metre.
R. Rare. Only a few isolated specimens found, less than 1 per sq. m.
N. None found after a search lasting half to one hour.
\+ Present, no information on frequency.

Observations in Germany, Holland and Belgium

Place	Date	Frequency	Notes	Observer
Cuxhaven	xii. 53	F	Probably settled after August 1953	Kühl
I. of Schiermonnikoog	viii. 51	N		den Hartog
	3. vi. 52	O	Settled in 1951	den Hartog
Noorderleegh	28. ix. 52	+	Settled 1951	Tulp
West-Torschelling	vii. 51	N		Mulder & Swennen
	14. viii. 51	R	One specimen on western mole of port	Schroevers
	Summer '51	O	In basin west of port	van Huissteden
	xi. 51	O	Beach Piles 13 to 16	Mulder
I. of Texel, Oude Schild	2. vii. 50	R	One specimen	Stock
	14. iv. 52	F	Many specimens	den Hartog
de Cocksdorp, Eyerland	3. viii. 51	F		Lucas
Near the Quarantaine, Wieringen	17. ii. 52	C		Swennen
Balgzand	4. viii. 51	R—O		den Hartog
Den Helder	19. xi. 50	+		Swennen
	30. iii. 51	O		Swennen
	21. xii. 51	F	Eastern part of dyke fairly free from *Elminius*	den Hartog & Swennen
Huisduinen	21. xii. 51	C		den Hartog & Swennen
Beach pile 8	5. i. 50	+		Swennen
Callantsoog	5. i. 50	C		den Hartog & Swennen
Hondsbosse Zeewering	19. ii. 50	R	Two specimens on breakwater	den Hartog & Mulder
	v. 50	R—O		den Hartog
	10. ix. 50	F	Rather numerous	den Hartog
	12. xi. 50	C	Very common	Stock

Place	Date	Frequency	Notes	Observer
Camperduin	22. i. 50	+	On a pier	Van der Goot
Ijmuiden	24. xii. 48	A	S. side of southern mole, very common	Stock
	x. 49	A	Northern mole	Mulder
	ii. 50	A	Both N. & S. moles	den Hartog & Mulder
	x. 50	A		Stock
	xi. 50	A		Mulder
Beach Pile 75	3. 1. 49	+		Mulder
Katwijk	28. x. 49	+	Sluice wall of Oude Rijn	Lucas
Wassenaarse Slag	19. x. 46	R	9 mm. specimen on wreck	Leenhouts & Lucas
	31. i. 48	R—O	On piles	Lucas & van Urk
Scheveningen	6. xii. 47	R	One specimen	Leenhouts
Between Kijkduin and Loosduinen	8. xii. 46	C	Largest specimens 8 mm. diam.	Van der Meulen
Kijkduin	18. x. 47	+	On a beach pile	Van der Meulen
Hook of Holland	16. x. 49	+	On northern mole	Lucas
I. of Goeree-Overflakkee	30. vii. 51	C	On western pier Ouddorp	Stock
S. of Goeree	3. viii. 51	F	On *Mytilus edulis*	Stock
The Westbout, Schouwen	10. viii. 48	R	One specimen on *Nucella lapillus*	Swennen
	24. viii. 50	C		den Hartog, Lucas & Mulder
Near Stompetoren	10. viii. 48	R	One specimen	Swennen
	23. viii. 50	F	Many specimens	den Hartog
Flauwers	17. viii. 50	+	On sluice	Stock
Dyke west of Zeirikzee	17. viii. 50	+		Stock
Dyke near the Kistersinlaag	26. viii. 50	C—A	Very many specimens	den Hartog, Lucas, Mulder & Swennen
Canal of Zierikzee	28. viii. 50	+		den Hartog
Beachpile near Watergat	x. 50	+		Viergever
Pier of Zierikzee	29. xi. 50	+		Viergever
Nr. Bruinisse, I. of Tholen	viii. 51	C	Many specimens	Mulder
Koffiehoek	ix. 50	R	One specimen	Viergever
	iii. 51	R		Viergever
	27. x. 51	F	Many specimens	den Hartog & Mulder
Gorishoek	28. x. 51	C		den Hartog & Mulder
Nr. Sophiapolder, Isle of N. Beveland	15. viii. 50	+		Stock
Kamperland	15. viii. 50	+	On landing bridge	Stock
Nr. Vlissingen, Isle of Walcheren	Autumn '49	F		De Vuyst
	9–12. viii. 50	+	On stones on beach, on pontoon and piles	den Hartog & Mulder
	xi. 51	+	On a pontoon	Mulder
Domburg	15. iv. 50	+	On *Mytilus edulis*	Van der Feen-van Bentham Jutting
	11. viii. 50	+	On pile works	den Hartog & Mulder

Place	Date	Frequency	Notes	Observer
Westkapelle	11. viii. 50	O	A few specimens	den Hartog & Mulder
Between Dishoek and Zoutelande	9. viii. 50	+		den Hartog & Mulder
Ritthem	13. viii. 50	+	On *M. edulis*, *L. littorea* and birchwood	den Hartog & Mulder
Rammekens	13. viii. 50	+	On wreck	Stock
Veere	13. viii. 50	+	Sluice and landing bridge	Stock
Yerseke Bank, Isle of Zuid Beveland	9. xi. 49	+		Korringa
Whole of East Schelt	1950	+		Local fishermen
Kattendijke, Yerseke and Zandkreek	30. viii. 51	A		Mulder
Katse Veer	22. viii. 50	C—A		den Hartog & Mulder
Wemeldinge	23. iii. 51	+		Mulder & Swennen
	30. viii. 51	A		Mulder
Canal gate, S. Beveland	4. x. 50	+	On a tunicate	Swaneveld
Ellewoutsdijk	3. viii. 50	C		den Hartog & Mulder
Mole, Borssele	4. viii. 50	C		den Hartog & Mulder
Mole, Hansweerd	10. viii. 50	+		Stock
Zeeuws Vlaanderen	12. viii. 50	+	Pier near Zwarte Polder	Stock
South of Cadzand	16. viii. 50	C		den Hartog & Mulder
Mole, Walsoorden	11. viii. 50	+		Stock
Bergen op Zoom	1950	+		Korringa
Ossendrecht	24. x. 51	O	On stakes on mudflats	den Hartog
Fort Lillo, Scheldt	1952	N	Only *B. improvisus*	Leloup & Lefevere
Coast of Belgium	1946–47	N		Leloup & Lefevere
Le Zoute	18. viii. 50	C	On piers	den Hartog
Zeebrugge Canal van Dudzele	18. viii. 50	C	A few specimens	den Hartog
S. of Mole near beach	19. viii. 50	A	Very large specimens	den Hartog & Mulder
Ostend	xi. 50	C	Found later on mussels collected by Research Vessel "Hinders"	Leloup & Lefevere
Ostend-Bruges Canal and	1952	+		Leloup & Lefevere
Belgian coast, south to Coxyde	1952	A	Up to 60 individuals on mussels 3 cm. long	

Observations in France and the Channel Islands.

Place	Date	Type of Shore	Habitat	Abundance	Max. size	Notes	Observer
Zuydcoote	9. 54	Dune coast	Wreck	F	5–6 mms.	Less common than *B. balanoides*	M.W.H.B. D.J.C.
Dunkerque	9. 54	Port	Port installations	F	6 mms.	much less than *B. balanoides*	M.W.H.B.
			Piles of inner basin of Port	O	mainly spat	,,	D.J.C.
Gravelines	9. 54	Dune coast	Wooden piers, stones, *Fucus*	C	8 mms.	More common at seaward end of pier	D.J.C.
Calais	9. 54	Port	Bassin Carnot	R			
			Avant Port	F	6 mms.	Less common than *B. balanoides*	M.W.H.B.
			Bassin à Flot	F			
			Stone breakwater	C		Commoner than *B. balanoides* Much spat	D.J.C.
		Dune coast	Stones	O	6 mms.	Less common than *B. balanoides*	M.W.H.B.
Cap Griz Nez	7. 51			F		20 specimens on a stone	den Hartog
Cap Blanc Nez	9. 54	Chalk cliffs and reefs	Base of cliff	R		*B. balanoides* also rare	D.J.C.
Audresselles	7. 51	Rocky slabs and sand	Rock	O—R		Six specimens	den Hartog
	9. 54		Rock	O	6 mms.	Much less than *B. balanoides* and very local	M.W.H.B. D.J.C.
Ambleteuse	7. 51			R		One specimen	Schroevers
Wimereux	9. 50	Broken rock and shingle	On rocks, *Mytilus* shells and stones	O		Much less common than *B. balanoides*	M.W.H.B.
	9. 54		Rock	R—O	Old specimens up to 11 mm.	,,	M.W.H.B. D.J.C.
Boulogne	7. 51		Northern mole	R		One specimen	den Hartog
	9. 54	Port	Pier	F		Much less common than *B. balanoides*	M.W.H.B.
			Avant Port	F	13 mms.	,,	M.W.H.B.
			Pont Marquet	O	12 mms.	,,	M.W.H.B.
		Estuary of R. Liane	Bridge over muddy river	F	8 mms.	Mostly dead with *B. improvisus* and *Hydroba ulvae*	D.J.C.

Place	Date	Type of Shore	Habitat	Abundance	Max. size	Notes	Observer
Le Portel	7. 51			+			Engel
Étaples	9. 54	Sandy muddy estuary	Rocks below bridge	N		*B. improvisus* only	M.W.H.B.
Berck-Plage	9. 54	Sand		N		No suitable substrates for barnacles	M.W.H.B.
Le Crotoy	9. 54	Sand and shingle		N		,,	M.W.H.B.
St. Valéry-sur-Somme	9. 54	Mud and sand		N		No barnacles	M.W.H.B.
Ault	9. 54	Chalk cliffs shingle and sand	Rock	O	9 mms.	Very local, less common than *B. balanoides*	M.W.H.B.
Mers	9. 54	Sand	Groynes	F	8 mms.	Common between settlements of *B. balanoides*	M.W.H.B.
Le Tréport	9. 54	Chalk cliffs and shingle	Base of cliffs	F	7 mms.	Mainly at H.W. mark	D.J.C.
		Harbour	Walls of harbour	O		Less than 5% of barnacle population	M.W.H.B.
		Estuary of Bresle River	Riverside	R	7 mms.	*B. balanoides* abundant	M.W.H.B.
		Shingle	Pier	O	6 mms.	,,	M.W.H.B.
Dieppe	9. 54	Port	Avant Port	O	Spat	,,	M.W.H.B.
					1–2/Sq. cm.		D.J.C.
					6 mms.		
			Derrière Port	O	6 mms.	As common as *B. balanoides*	M.W.H.B.
					a few 11 mm.		
			Pier	R	12 mms.	Much less than *B. balanoides*	M.W.H.B.
		Boulders at base of chalk cliff	Boulders	O	9 mms.	Less than *B. balanoides*	D.J.C.
St. Valéry-en-Caux	9. 54	Shingle, sand and chalk cliff	Concrete groyne	O	Mostly spat 2–4 mms.	,,	M.W.H.B.
			Harbour walls	R	Mostly last year's spat	Much less than *B. balanoides*	M.W.H.B.
Fécamp	9. 54	Stones, shingle and chalk cliffs	Bassin à flot	R		Much *B. balanoides* and *B. improvisus*	M.W.H.B.
			Harbour entrance sheltered side	R	4 mms.		M.W.H.B.
			Exposed side	R	10 mms.	Mainly small ones	M.W.H.B.
			Beach	O	Spat only		D.J.C.
Etretat	9. 54	Chalk cliff shingle and rock reef	Rock	F	8 mms.		M.W.H.B. D.J.C.
Ste. Adresse	9. 54	Shingle beach	Breakwaters	C		Less than *B. balanoides*	M.W.H.B.
Le Havre	9. 53	Port	Wreckage from tidal harbour	A			M.W.H.B.

			Beach	O	Spat only		D.J.C.
Etretat	9. 54	Chalk cliff shingle and rock reef	Rock	F	8 mms.		M.W.H.B. D.J.C.
Site. Adresse	9. 54	Shingle beach	Breakwaters	C		Less than *B. balanoides*	M.W.H.B.
Le Havre	9. 53	Port	Wreckage from tidal harbour	A			M.W.H.B.
	9. 54		Harbour installation	A		Commoner than *B. balanoides*	D.J.C.
Bac du Hode	9. 54	Estuary	Pier piles examined	N		No barnacles found	M.W.H.B.
Honfleur	9. 54	Estuary	Harbour entrance	A	10 mms.	With *B. improvisus*	M.W.H.B. D.J.C.
			Harbour	R	Very small		M.W.H.B.
Trouville	9. 54	Estuary	River side	A		Close packed and elongated. Much commoner than *B. balanoides*	M.W.H.B.
		Bassin à flot	Dock wall	A	12 mms.	Dominant species	M.W.H.B.
Deauville	9. 54	Sand	Pier piles	A		*B. balanoides* almost excluded	M.W.H.B.
			Rocks	A		*B. balanoides* smothered	D.J.C.
Houlgate	9. 54	Sand	Groynes	A		*B. balanoides* very rare, dead	M.W.H.B.
Cabourg	9. 54	Sand	Stones	C		*Elminius*, only on abraided stones, mean sea level	D.J.C.
Franceville-Plage	9. 54	Sand		N		No suitable substrates	M.W.H.B.
River l'Orne, Pegasus bridge	9. 54	River	Stones	O	Large	With *B. improvisus*	M.W.H.B.
Riva-Bella	9. 54	Sand		N		No suitable substrates	M.W.H.B.
Luc-sur-Mer	9. 54	Sandy	Rocks and groynes	C	all sizes	Heavy settlement occurring, but less common than *B. balanoides*	M.W.H.B.
Arromanches (Port Winston)	9. 54	Sand and small rocks	Pontoons, etc. of Mulberry Harbour	O	14 mms.	Less than *B. balanoides*, mainly in shelter	M.W.H.B.
		Eroded soft cliff to west	Rocks	O		Few adults, mainly spat	M.W.H.B. D.J.C.
Port-en-Bessin	9. 54	Port	Inner harbour	O	Large	With *B. balanoides*	M.W.H.B.
			Outer harbour	F—O	14 mms. (high up)	Less common than *B. balanoides*, many cyprids.	M.W.H.B.
		Headland	Rocks	N		Abundant algae, few barnacles	M.W.H.B.
St. Laurent-sur-Mer (Omaha Beach)	9. 54	Dune coast	Wrecks	A	all sizes	Both *Elminius* and *B. balanoides* very abundant	M.W.H.B.
Pointe du Hoc	9. 54	Rocky headland	Rocks & boulders	C		Less common than *B. balanoides*	D.J.C.
Grandcamps-les-Bains	9. 54	Sand and shingle	Harbour walls	F	Large	,,	M.W.H.B.
			Stones on beach	C	13 mms.	More common than *B. balanoides*	D.J.C.
			Pier Piles				M.W.H.B.
Insigny	9. 54	Muddy estuary	Near road bridge	F	Large	No other species present	M.W.H.B.
St. Marie du Mont (Utah Beach)	9. 54	Sand	Wrecks	A		Much *B. balanoides* also	M.W.H.B.

Place	Date	Type of shore	Habitat	Abundance	Max. size	Notes	Observer
Quinéville	9. 54	Sand	Breakwaters	A	12 mms.	Much commoner than *B. balanoides*	D.J.C.
St. Vaast la Hougue	9. 54	Rocks and mud	Harbour walls	C	Large	Commonest species in shelter	M.W.H.B.
			Rocks	F		Much weed cover	D.J.C.
Barfleur	9. 54	Rocks, mud and sand	Rock	O		,,	D.J.C. M.W.H.B.
			Inner harbour	R	Large	About equally as common as *B. balanoides*	M.W.H.B.
			Outer harbour	C		,,	M.W.H.B.
Pnte de Barfleur	9. 54	Rocky headland	Rock near H.W. mark	R	9 mms.	Heavy algal growth, few barnacles	M.W.H.B. D.J.C.
Cap Lévy	9. 54	,,	Rocks & boulders	R	11 mms.	*B. balanoides* abundant	M.W.H.B. D.J.C.
Fermanville	9. 54	Rocky coast	Harbour	O	8 mms.	,,	M.W.H.B.
Bretteville	9. 54	,,	Rocks	O			D.J.C.
Cherbourg	9. 54	Port	Boulders on beach	F	Large	Fewer than *B. balanoides*	M.W.H.B.
			Harbour wall	C	12 mms.	Commoner than *B. balanoides*, 50% infected by *Hemioniscus balani*	D.J.C. M.W.H.B.
			W. corner of harbour	C	11 mms.		M.W.H.B.
Nacqueville	9. 54	Sand with rocks at L.W.	Rocks	O		Less than *B. balanoides*	D.J.C.
Eculleville	9. 54	Rocky	Rocks towards H.W.	R			D.J.C.
Omonville-la-Rogue	9. 54	Large boulders, rock and stones	Rocks	R	11 mms.	With *B. balanoides*	D.J.C. M.W.H.B.
			Harbour	R		,,	M.W.H.B.
Anse St. Martin	9. 54	Rock, sand and shingle	Rocks	R		,,	M.W.H.B.
			Inside Harbour	N		,,	M.W.H.B.
Cap de la Hague (Goury la Hague)	9. 54	Rock and boulder	Rocks	O—R		,,	D.J.C.
			Harbour	R	8 mms.	,,	M.W.H.B.
Vauville	9. 54	Rock, sand and shingle	Rock	O			
Siouville	9. 54	Sand and reefs	Rock	R		At High Water mark only	M.W.H.B.
Carteret	9. 54	Sand and rock	Harbour	N		*B. balanoides* only	M.W.H.B. D.J.C.
			Rocks	N			M.W.H.B. D.J.C.
Lindbergh Plage	9. 54	Sand		N		No suitable substrates for barnacles	M.W.H.B.
Bretteville-sur-Ay	9. 54	Sand		N		,,	M.W.H.B.

		Rocks	N			D.J.C.
Lindbergh Plage	9. 54	Sand		N	No suitable substrates for barnacles	M.W.H.B.
Bretteville-sur-Ay	9. 54	Sand		N	,,	M.W.H.B.
Créances	9. 54	Sand and salt marsh		N	,,	M.W.H.B.
Armanville Plage	9. 54	Sand		N	,,	M.W.H.B.
La Portière	9. 54	Sand		N	,,	M.W.H.B.
Blainville	9. 54	Low reefs in sand	Rocks	N	*B. balanoides* present	M.W.H.B.
			Estuary	N	No barnacles	M.W.H.B.
Coutainville	9. 54	Low reefs in sand	On large stones	R		D.J.C.
Heugueville le Prey	9. 54	Estuary	Bridge	N	Apparently suitable environment but no barnacles	M.W.H.B.
Alderney						
Clonque Fort	9. 56	Rocky shore	Sheltered and exposed reefs examined	N.		A. J. Southward
Pt. Grosney	9. 56	Exposed rocky shore	Rocks examined	N		,,
Braye harbour	9. 56	Sheltered harbour and beach	Various substrata examined	N		,,
Pt. Quesnard	9. 56	Exposed shore	Sandstone reefs examined	N		,,
Longey Bay	9. 56	Boulder, sand and gravel	Boulder examined	N		,,
Telegraph Bay	9. 56	Boulders, somewhat scoured	,,	N		,,
Guernsey						
St. Peter Port	9. 56	Harbour area	Various substrata examined	N		,,
Fort Doyle	9. 56	Fairly exposed rocky coast	Rocks examined	N		,,
Grand Camp	9. 56	Boulders and rock	Boulders and outer reefs	N		,,
Isle Lihou	9. 56	Flat rocky shore	Rocks examined	N		,,
La Moye Pt.	9. 56	Steep rocky shore	,,	N		,,
Jerbourg Pt.	9. 56	,,	Sheltered port and rocks examined	N		,,
Jersey						
Montorgueil Castle	9. 56	Steep rocky shore, rising from boulder and sand	Rocks and boulders examined	N		

Place	Date	Type of Shore	Habitat	Abundance	Max. size	Notes	Observer
Elizabeth Castle	9. 56	Sheltered reefs	Rocks examined	N			A. J. Southward
Frémont Pt.	9. 56	Exposed rocky point	,,	N			,,
Plémont Pt.	9. 56	Rocky shore	,,	N			,,
La Corbière	9. 56	Broken rocky shore sand and boulder	Rocks and boulder	N			,,
Regneville	9. 54	Sandy estuary		N		No suitable substrates. No barnacles	M.W.H.B.
Salines	9. 54	Brackish marsh	Stones	N		Suitable stones present, but no barnacles	M.W.H.B.
Granville	9. 54	Rocky with shingle	Reef	N		Many barnacles	D.J.C.
							M.W.H.B.
			Harbour	R		Two specimens	M.W.H.B.
St. Jean-le-Thomas	9. 54	Sand and boulder		N			D.J.C.
Portaubault	9. 54	Estuary		N		Bridge appeared suitable substratum, but no barnacles	M.W.H.B.
Le Mont St. Michel	9. 53	Rocks	Rocks examined	N		No barnacles found	M.W.H.B.
Port Briac, Cancale	9. 54	Sheltered rocky shore		N		Much weed cover	D.J.C.
Rotheneuf	9. 54	Rocky shore		N			D.J.C.
St. Malo	9. 54	Rocky coast	Headlands	N		Many barnacles	M.W.H.B.
		Avant Port	Harbour wall	R	10 mms.	One large specimen	M.W.H.B.
			Boat hull	R		One specimen	M.W.H.B.
			Jetty	N		Many barnacles	M.W.H.B.
			Wreck	N			M.W.H.B.
	8. 55	Rocky coast	Headlands, Rocks examined	N			M.W.H.B.
		Port Area	Avant Port, Harbour walls	N			M.W.H.B.
			Disused lock	R			M.W.H.B.
			Harbour	N		Many barnacles	M.W.H.B.
			Beached craft etc.	R			M.W.H.B.
St. Servan	9. 54	Sheltered sandy estuary	Harbour	N		Many barnacles	M.W.H.B.
	8. 55		Rocks	N			M.W.H.B.
			Local craft	N			M.W.H.B.
			Mussels served in restaurant !	R			M.W.H.B.
			Rocks in bay to south of St. Servan	N		Apparently suitable site	M.W.H.B.
La Passagère	8. 55	Muddy and rocky	Rocks	N		,,	M.W.H.B.
St. Suliac	9. 54	Estuary	Jetty and rocks	R		One specimen 4 mm.	M.W.H.B.
Port St. Jean	9. 54	Estuary	Stones and concrete blocks	R	10 mms.	Three specimens only other barnacles frequent	M.W.H.B.

			restaurant !				
			Rocks in bay to south of St. Servan	N		Apparently suitable site	M.W.H.B.
	La Passagère	8. 55	Muddy and rocky	Rocks	N	,,	M.W.H.B.
	St. Suliac	9. 54	Estuary	Jetty and rocks	R	One specimen 4 mm.	M.W.H.B.
	Port St. Jean	9. 54	Estuary	Stones and concrete blocks	R	10 mms. Three specimens only other barnacles frequent	M.W.H.B.
	La Hisse	9. 53 9. 54	Estuary	Rocks under bridge	N	Too fresh for barnacles ?	M.W.H.B.
	Port St. Hubert	9. 53	Estuary	Rocks	R	One specimen after long search	M.W.H.B.
	Montmarin	9. 53	Estuary	Rocks examined	N	Many barnacles	M.W.H.B.
	La Landriais	9. 53	Estuary	Rocks examined	N	Many barnacles	M.W.H.B.
	Plage du Prieure, Dinard	9. 54	Rocky estuarine	Rocks examined	N	*Chthamalus* and *Balanus* abundant	M.W.H.B.
	Dinard	9. 53	Exposed rocky coast	,,	N	,,	M.W.H.B.
		9. 54		,,	N	,,	M.W.H.B.
	St. Lunaire	9. 53	,,	,,	N	,,	M.W.H.B.
	St. Briac	9. 54	Muddy estuary	,,	N	Apparently suitable habitat	M.W.H.B.
	Beaussais	9. 54	Sandy and muddy bay		N	No suitable substrates for barnacles	M.W.H.B.
	Notre Dame-du-Guildo	9. 54	Estuary	Road Bridge	R	One specimen 9 mms.	M.W.H.B. D.J.C.
	Le Port à la Duc	9. 54	Muddy bay with rocks	Rocks examined	N	No barnacles	M.W.H.B.
	Cap Fréhel	9. 54	Rocky headland	Both sides of headland examined	N		D.J.C.
	Erquy-Pages	9. 53	Rocks and sand	Harbour wall	N	Many barnacles	M.W.H.B.
		9. 54			N		D.J.C.
	Pte. de Pléneuf	9. 54	Rocky headland	Rocks examined	N		D.J.C.
	La Val André	9. 54	Dirty estuary	Bridge examined	N	*B. balanoides* ·05/sq. cm.	D.J.C.
	La Mane-Noire (Anse d'Yffiniac)	9. 54	Mud and saltmarsh		N	No suitable substrata	M.W.H.B.
	St. Ilan (,,)	9. 54	,,		N	,,	M.W.H.B.
	Cesson	9. 54	Estuarine polluted	Harbour walls and rocks examined	N	A few *Chthamalus* only	D.J.C.
	Pte. du Roselier	9. 54	Steep rocky coast	Rocks examined	N		D.J.C.
	Binic	9. 54	Harbour estuarine	Under road bridge of R. Ic.	N	A few *Chthamalus*	M.W.H.B.
				Harbour wall	R	6 mms. One specimen, other barnacles abundant	M.W.H.B.
				Inner harbour	N	Other species abundant	M.W.H.B.

Place	Date	Type of Shore	Habitat	Abundance	Max. size	Notes	Observer
St. Quay-Portrieux	9. 53	Rocks and sand	Rocks examined	N			M.W.H.B.
	9. 54			N			D.J.C.
Paimpol	9. 53	Mud and sand	Harbour	N		No barnacles	M.W.H.B.
L' Arcouest	9. 53	Rocky, sheltered	Rocks examined	N		Other species abundant	M.W.H.B.
Lezardrieux	9. 54	Muddy estuary of the Trieux	Rocks, jetty and bridge examined	N		Mainly *B. balanoides*	M.W.H.B. D.J.C.
Sillon de Talbert	9. 54	Flat reef of boulder and rock	Rocks and stones examined	N			D.J.C.
Tréguier	9. 54	Muddy estuary of Jaudy	Road bridge and boulders at all levels	C	10 mms.	Well established, about 0·8/sq. cm., with *B. balanoides*, *B. improvisus*, *B. crenatus*, *B. perforatus*, and *Chthamalus*	D.J.C.
Perros Guirec	9. 54	Rock and sand	Harbour walls in shelter	R		Little recent settlement	M.W.H.B.
Trestrignel Plage	9. 54	Rocks and sand	Rocks examined	N		Many barnacles	M.W.H.B.
Trégastel Plage	9. 54	Sand and boulders	Rocks examined	N			D.J.C.
Lannion	9. 54	River	Stone river walls	F	Large specimens	Water of very low salinity	M.W.H.B.
Le Yaudet	9. 54	Estuary	Rocks	F	Mostly 4 mms.	About 1% of barnacle population	M.W.H.B.
St. Michel-en-Grève	9. 54	Sandy bay, rocky headlands	Wooden posts examined	N			D.J.C.
St. Efflam	9. 53	Sandy bay		N			M.W.H.B.
Primel-Trégastel	9. 54	Exposed rocky	Rocks examined	N			D.J.C.
			Sheltered bay	C		Commoner than *B. balanoides* but less common than *Chthamalus*	D.J.C.
Morlaix	9. 53	Narrow muddy estuary	Rocks, river wall, buoys on quayside	C	9 mms.	No other barnacles on rocks and river wall	M.W.H.B.
	9. 54	"	"	C	10 mms.	*B. improvisus* and *perforatus* and *Verruca* on buoys	M.W.H.B.
Penzé	9. 53	Small estuary	Wood, stones	C		No other barnacles	M.W.H.B.
Roscoff	9. 53	Rocky coast	Bay	O		Heavy algal growth, few barnacles	M.W.H.B.
			Harbour	A	8 mms.	Some recent settlement	M.W.H.B.
St. Pol-de-Léon	9. 53	Sheltered bay	Rocks	C			M.W.H.B.
Keremma	9. 53	Rocks and sand	Rocks	F	6 mms.	With *Chthamalus* and *B. balanoides*	M.W.H.B.
Pnte. de Pontusval	9. 54	Rock and sand	Rocks	R			D.J.C.
Guissény	9. 53	Small estuary	Rocks	O		Few barnacles	M.W.H.B.
Grèves du Vougot	9. 54	Rocky reef and sand	Rock	R			D.J.C.
Aber-Wrac'h	9. 53	Estuary	Road bridge	O	Large	Only species found	M.W.H.B.

Pnte. de Pontusval	9. 54	Rock and sand	Rocks	R			D.J.C.
Guissény	9. 53	Small estuary	Rocks	O		Few barnacles	M.W.H.B.
Grève du Vouget	9. 54	Rocky reef and sand	Rock	R			D.J.C.
Aber-Wrac'h	9. 53	Estuary	Road bridge	O	Large	Only species found	M.W.H.B.
	9. 54	,,	,,	C			D.J.C.
Tréglonou	9. 53	Sandy and muddy estuary	,,	C	17 mms.	With *B. balanoides* and *improvisus*	M.W.H.B.
	9. 54	,,	,,	A	15 mms.	,,	D.J.C.
Trémazan	9. 54	Exposed shore	Rocks examined	N		Algae abundant, barnacles few	D.J.C.
Lanildut	9. 53	Muddy estuary	Rocks	O		Only species found	M.W.H.B.
Le Conquet	9. 54	Sandy bay, rocky headlands	Rocks examined	N			D.J.C.
			Harbour	R		One only found	D.J.C.
Pnte. du Grand Minou	9. 54	Rocky promontory	Rocks	O			D.J.C.
Penfeld	9. 53	Small muddy estuary	Under bridge	F	14 mms.	Only species found	M.W.H.B.
Brest	9. 53	Port	Rocks near Pont Albert Louppe	A	Small 5 mms.		M.W.H.B.
Daoulas	9. 53	Estuary	On stones	A	Large	With *B. improvisus*	M.W.H.B.
l'Hôpital-Camfrout	9. 53	Estuary		F		Only species found	M.W.H.B.
Pont de Térénez	9. 53	Estuary		A		With *B. balanoides*	M.W.H.B.
Roscanvel	9. 53	Rocky coast	Rocks	C	Small	With *Chthamalus* and *B. balanoides*	M.W.H.B.
Pnte. des Espagnols	9. 53	Rocky	Rocks	C	Small	With *Chthamalus* and *B. balanoides*	M.W.H.B.
Mort d'Anglais	9. 53	Sheltered rocky bay	Rocks	N		*Chthamalus* very abundant	M.W.H.B.
Camaret	9. 53	Sheltered harbour	Harbour wall	R	5 mms.		M.W.H.B.
Morgat	9. 53	Sheltered harbour on rocky coast	,,	R	11 mms.	*Chthamalus* very abundant	M.W.H.B.
			Rocks examined	N		,,	M.W.H.B.
Douarnenez	9. 53	Port and rocky bay	Harbour area examined	N			M.W.H.B.
			Estuary	R	9 mms.	With *Chthamalus*	M.W.H.B.
			Rocks	N			M.W.H.B.
	9. 54		Harbour walls examined	N			D.J.C.
			Rocks examined	N			D.J.C.
Pnte. du Raz	9. 54	Exposed headland	Rocks examined	N			D.J.C.
Pnte. de Lervily	9. 54	Boulder and rock	Rocks examined	N			D.J.C.
Pont-Croix	9. 53	Estuary	Bridges examined	N		Ideal habitat but no barnacles	M.W.H.B.

Place	Date	Type of Shore	Habitat	Abundance	Max. size	Notes	Observer
Audierne	9. 53	Harbour	Harbour walls examined	N			M.W.H.B.
	9. 54	,,	Harbour wall	R		One specimen	D.J.C.
St. Guénolé	9. 54	Exposed headland	Rocks examined	N			D.J.C.
Pont-l'Abbé	9. 53	Dirty estuary	Under mill and on rocks	R	14 mms.	No recent settlement	M.W.H.B.
Bénodet	9. 53	Sheltered estuary	Rocks examined	N		Good habitat for *Elminius*	M.W.H.B.
La Forêt	9. 53	Estuary	Rocks	N		,,	M.W.H.B.
Concarneau	9. 53	,,	Harbour walls examined	N		,,	M.W.H.B.
	9. 54	,,	,,	N		*B. crenatus* and *B. perforatus* abundant	D.J.C.
Pnte. de Trévignon	9. 54	Rocky headland	Boulders and rock examined	N			D.J.C.
Belon estuary	9. 53	Estuarine		N		Good habitat for *Elminius*	M.W.H.B.
Le Pouldu	9. 53	,,		N		,,	M.W.H.B.
Lorient, La Rade	9. 53	Estuary and port	Large stones examined	N		Rather few barnacles	M.W.H.B.
Lorient, Estuary of Scorff	9. 53	Estuary	Below road bridge	R	14 mms.	Three specimens only	M.W.H.B.
Kerentrée	9. 54	Estuarine and marshy	Rocks and bridge examined	N		Apparently suitable habitat for *Elminius*	M.W.H.B.
St. Colombier	9. 54	,,		N		*B. improvisus* only	M.W.H.B.
Kerners	9. 54	Sheltered bay of inland sea	Bridge and rocks	N		Apparently a good habitat for *Elminius*	M.W.H.B.
Pnte. Navalo	9. 54	Rock and sand and boulder	Rocks and breakwater	N		*Verruca*, *B. balanoides* and *Chthamalus* present	M.W.H.B. D.J.C.
Arzon	9. 54	Muddy bay		N		No barnacles found	M.W.H.B.
St. Gildas de Rhuis	9. 54	Rocky shore	Rocks examined	N			D.J.C.
Pnte. de Penlan	9. 54	Muddy and estuarine	Rocks examined	N			D.J.C.
La Roche-Bernard	9. 54	Muddy estuary	Bridge	N		No barnacles found	M.W.H.B. D.J.C.
Le Croisic	9. 54	Rocky shore	Rocks examined	N			D.J.C.
St. Marc	9. 54	,,	,,	N		*Chthamalus* and *B. balanoides* common	M.W.H.B.
St. Nazaire	9. 54	Port	Rocks and harbour walls	N		*B. balanoides* and *B. improvisus*	M.W.H.B.
Blindin	9. 54	Muddy sandy estuary	Jetties examined	N		,,	M.W.H.B.
St. Michel-Chef-Chef	9. 54	Sand with a few	Rocks and	N		*B. improvisus* present	D.J.C.

			,,		*Chthamalus* and *B. balanoides* common	M.W.H.B.
St. Nazaire	9. 54	Port	Rocks and harbour walls	N	*B. balanoides* and *B. improvisus*	M.W.H.B.
Mindin	9. 54	Muddy sandy estuary	Jetties examined	N	,,	M.W.H.B.
St. Michel-Chef-Chef	9. 54	Sand with a few rocks	Rocks and mussels	N	*B. improvisus* present	D.J.C.
Pornic	9. 54	Estuary and Harbour	Harbour walls	N	Few barnacles in harbour; plenty in estuary	M.W.H.B.
Port du Bec	9. 54	Port in canal	Canal walls examined	N	No barnacles found	M.W.H.B.
La Bernerie-en-Retz	9. 54	Sand and reefs	Rocks examined	N	*Chthamalus*, *B. balanoides* and *B. improvisus*	M.W.H.B.
Notre-Dame-de-Monts	9. 54	Sand		N	No suitable substrates for barnacles	M.W.H.B.
Sion-sur-l'Ocean	9. 54	Exposed rocks	,,	N		D.J.C.
Croix-de-Vie	9. 54	Rocky and sandy reef	,,	N		D.J.C. M.W.H.B.
St. Gilles-sur-Vie	9. 54	Estuary and Harbour	Stones, harbour wall, boats	N	*B. improvisus* present	D.J.C. M.W.H.B.
Les Sables d'Olonne, Pnte. de l'Aiguillé	9. 54	Rocky coast	Rocks examined	N		D.J.C.
Les Sables d'Olonne, Harbour, La Chaume	9. 54	Dirty enclosed harbour	Harbour walls	N	*B. amphitrite*, *B. perforatus* and *Chthamalus* only	D.J.C. M.W.H.B.
		Beach area	Slipways, boats, etc.	N	*B. amphitrite* frequent	M.W.H.B.
Les Sables, Le Puits d'Enfer	9. 54	Rocky shore	Rocks examined	N		M.W.H.B.
La Pallice	9. 54	Rock and boulder	Slipway and rocks	N		D.J.C.
			Harbour	N		D.J.C.
La Rochelle	9. 54	Port	Inner non-tidal basin	N	*B. amphitrite* present	M.W.H.B.
			Canal	N	,,	M.W.H.B.
			Avant Port, and boats	N	,,	M.W.H.B.
			Stones on beach	N	,,	M.W.H.B.
Pnte. du Rocher	9. 54	Sand and stones	Stones and wooden stakes examined	N	*B. improvisus* and *amphitrite*	D.J.C.
Fouras	9. 54	Sand and boulder	Boulder examined	N		D.J.C. M.W.H.B.
L'Eguille	9. 54	Muddy river		N	No barnacles found	M.W.H.B.
Ronce-les-Bains	9. 54	Sand and boulder	Boulders examined	N		D.J.C.
La Grande Côte	9. 54	Exposed rocks	Rocks and mussels	N		D J.C.

Place	Date	Type of Shore	Habitat	Abundance	Max. size	Notes	Observer
St. Palais-sur-Mer	9. 54	Rock and boulder	Rocks examined	N			D.J.C.
Royan	9. 54	Rock and sand	Rocks examined	N		Mainly *B. improvisus* and *B. perforatus*	D.J.C. M.W.H.B.
St. Georges-de-Didonne	9. 54	Reefs and sand	Rocks and stones	N		,,	D.J.C.
Meschers	9. 54	,,	,,	N			D.J.C.
Pnte. de Grave	9. 54	Sandy with rocks	Rocks examined	N		*B. improvisus* present	M.W.H.B.
Soulac	9. 54	Sand		N		No suitable substrates, no barnacles	M.W.H.B.
Hourtin-Plage	9. 54	Sand		N		,,	M.W.H.B.
Cap-Ferret	9. 54	Stony and sandy	Rocks and pier piles	N		Mainly *B. perforatus* and *Chthamalus*	D.J.C.
Piquey-Plage	9. 54	,,	Rocks and stones	N			D.J.C.
Arès	9. 54	Sandy	Jetty examined	N		No barnacles found	M.W.H.B.
Taussat-les-Bains	9. 54	Muddy with *Zostera*	Boat bottoms	N		*B. perforatus* and *B. improvisus* only	D.J.C.
Arcachon	9. 54	Sandy and artificial concrete works	Piers and boats examined	N		*B. perforatus* and *Chthamalus* mainly	D.J.C. M.W.H.B.
Pyla-sur-Mer	9. 54	Sand	Breakwaters and concrete blocks	N		*B. improvisus* found	M.W.H.B.
Mimizan-Plage	9. 54	Sandy estuary	River walls and piers	N		*Chthamalus* mainly	D.J.C.
Labenne-Plage	9. 54	Sand	Derelict concrete blocks examined	N		*Chthamalus* only	D.J.C. M.W.H.B.
Bayonne	9. 54	Estuarine	River banks etc.	N		No barnacles found	M.W.H.B.
Chambre d'Amour	9. 54	Reefs and sand	Rock examined	N			D.J.C.
Biarritz	9. 54	Rocky coast with sandy bays	Rocks and harbour examined	N		*B. amphitrite* present	D.J.C. M.W.H.B.
St. Jean-de-Luz	9. 54	Rocky bay	Rocks at eastern end in shelter	N			D.J.C. M.W.H.B.
			Inner harbour	R		Single large specimen only. *B. amphitrite* and *B. eburneus* present	M.W.H.B.
			R. Nivelle	N			M.W.H.B.
			Beach area	N			M.W.H.B. D.J.C.
Socoa	9. 54	Exposed reefs and cliffs	Rocks	N			D.J.C. M.W.H.B.
Hendaye	9. 54	Sand and rock	Port area and rocks examined	N			M.W.H.B.

ADAPTIVE FEATURES IN THE SKULLS OF AFRICAN SUIDAE

BY

R. F. EWER

Department of Zoology, Rhodes University, Grahamstown

[Accepted 4th December 1956]

(With 3 plates and 9 figures in the text)

CONTENTS

		Page
I.	Introduction	135
II.	The Bushpig and the Warthog	136
	1. Feeding habits	136
	2. The muscles	139
	3. Offence and defence	145
	4. Skull architecture	149
III.	The skull of the forest hog, *Hylochoerus*	151
IV.	Fossil species	153
V.	Summary	154
VI.	Acknowledgments	154
VII.	References	155

I. INTRODUCTION

In any study of fossil species it is desirable to understand in functional terms the evolutionary trends which are manifested, and to deduce as much as possible about the modes of life of the animals. Such an understanding can best be acquired by a study of related extant species, where it is possible to correlate bony structure with musculature and bones and muscles with habits.

In the evolution of the African Suidae one of the most important trends in the dentition has been the change of the molars from low-crowned bunodont teeth, of the type associated with an omniverous feeding habit, to high-crowned, cement-covered, multicusped teeth of the type normally found in grazing animals. Along with this elaboration of the molars goes reduction in the premolars and incisors. The associated changes in skull architecture are not very clearly understood. It therefore seemed desirable to make a study of the skulls and cranial musculature of the two extant South African species, in relation to their habits and modes of feeding.

The species in question are the Bushpig, *Potamochoerus koiropotamus* (Desm.), and the Warthog, *Phacochoerus africanus* (Gmelin). They differ widely in dentition, skull architecture and feeding habits ; and a study of two so diverse types may be expected to be of considerable assistance to our understanding of suid evolutionary trends.

II. THE BUSHPIG AND THE WARTHOG

1. *Feeding habits*

(a) *Bushpig*

The feeding habits of this species are well known, and there are no serious differences of opinion amongst the various authors who have written on the subject. The Bushpig is extremely omnivorous, taking animal as well as vegetable food, and roots and bulbs form a very important part of its diet. These are dug up with the snout,* and in any area inhabited by Bushpig extensive turning over of the soil will always be found. Phillips (1926) gives an excellent account of its feeding habits and details may be found in his paper. In addition, most of the authors quoted below in the section on Warthog feeding habits refer also to Bushpig. For the present purpose it is sufficient to characterise the Bushpig as an omnivore, in which digging with the snout constitutes an essential element in the method of obtaining food.

It was not possible for me to make any personal observations on the behaviour of the Bushpig, and their method of chewing has therefore not been directly observed. However, the wear of the canines against each other produces vertical scratches, and the cheek teeth are not worn flat, but show a tendency for transverse ridging. Both of these facts would seem to indicate that the jaw action is mainly a simple chopping one, without very marked grinding in either the orthal or the propalinal direction.

(b) *Warthog*

On the question of Warthog feeding habits the following authors have been consulted : Kirby (1896, 1899). Roosevelt (1910), Woodhouse (1911), Roosevelt & Heller (1914), Stevenson-Hamilton (1947), Copley (1949) and Watson (1949). A number of the authors of collective works, such as Fitzsimons (1920) and Shortridge (1934) seem to have gathered their information largely from Kirby, Roosevelt and Roosevelt & Heller. The general consensus of opinion is that the Warthog is essentially a grazer, living in much drier and more open country than the Bushpig, and shunning densely forested areas. Opinions differ as to the importance of digging up of roots, and it is generally held that in digging both the rhinarium and the tusks are used. The importance of digging appears to depend on local conditions, varying with the relative abundance of fresh grass and of suitable roots and bulbs. The available water supply also seems to be important in this respect, for juicy roots and bulbs may be much sought after if water is not available. From a study of the literature it appears that grass is preferentially taken, and there is general agreement that the digging of roots and bulbs is of much less importance than in the case of the Bushpig. It thus appears that the Warthog is mainly a grazer, although showing considerable adaptability in its feeding habits in accordance with the exigencies of local conditions. The extreme case of this

* Although the rhinarium is the most important digging organ the tusks may be used to some extent : it would, in fact, be impossible for more than a very shallow excavation to be made without the canines becoming involved. The rounding off of the external edge of the tip of the upper tusk is presumably the result of wear incidental to digging.

adaptability is shown by a population of this species in Senegal, described by Guiraud (1948). In this particular case the Warthog were living in a damp, heavily bushed area, behaving very much as Bushpig usually do, and feeding extensively on roots. No other author has described Warthog living in this manner, and the case must be regarded as exceptional.

The specialised multicusped hypsodont third molars and reduced premolars of the Warthog accord with its characterisation as a grazing animal ; but the reduction of the incisors is difficult to understand.* They appear quite unsuited to the cropping of grass, and are very different from the horizontal cutting blade formed by the lower incisors of the grazing Bovidae. No discussion of this point could be found in the literature, and an understanding of the adaptational significance of the reduced incisors therefore necessitated a study of the habits of the animal in natural conditions.

For this purpose a visit was paid to the Hluhluwe Game Reserve in Northern Zululand. Here Warthog are abundant, and their freedom from attack by man renders them relatively easy to watch. The observations recorded below were made in January : while it is true that the food taken may be different at other times and in other areas, the methods of cropping and of chewing are unlikely to show such variation.

(1) *Foods taken*

Every day during the ten-day period of observation numerous groups of Warthog were observed feeding. Two family groups payed several visits to a wild fig tree and fed on the fallen fruit, but apart from this, the only food taken was short grass. Long grass, herbaceous plants and bark were not eaten, and I did not see any animal digging up roots or bulbs. The Game Rangers confirm that in this Reserve the Warthog do not dig to any noticeable extent, and although plenty of long grass is available, they feed only on the short grass.

The stomach contents of one animal which was found killed consisted of grass only. Seven samples of droppings were collected and examined microscopically. The only identifiable material in each case was grass. Droppings of 'Nyala, *Tragelaphus angasii* Gray (Bovidae), were also examined, and were found to contain a higher proportion of finely ground unidentifiable material, small pieces of grass blades and a considerable amount of finely chopped stems of herbaceous plants.

(ii) *Method of cropping,*

In natural conditions a pure stand of grass is not common, and in the short grass where the Warthog were observed to feed, many small dicotyledonous plants (" weeds ") were always present together with the grass. The Warthog show extreme selectivity in their feeding, and examination of an area which an animal has just worked over shows that only the close growing young tips of the grass have been removed, the weeds being untouched. As the animal feeds the head is moved gently back and forth and then a bite is nipped off with a slight jerk of the head. The back-and-forth movement

* Descriptions of the dentitions of the Warthog and Bushpig may be found in Cooke (1949).

appears to brush aside the unwanted weeds and allow the animal selectively to pluck out the grass tips. Even when feeding on the grass of the Game Conservator's lawn the same selectivity was shown. The back-and-forth movements were made, and only the tender growing tips were plucked. I was impressed time and again by the small amount of material removed by the Warthog. The significance of the reduced incisors is now apparent : the animal is not cropping as a sheep crops, but is using its small inwardly pointing incisors like a pair of tweezers to pluck out the selected food, and reject the unwanted material.

Dr Leakey informs me that in dry weather, when grass is scarce, Warthog often feed on tufts of grass growing at the base of thorny bushes and thus not easily accessible to ordinary grazers. The back-and-forth movements are used to push aside the unwanted vegetation and work the snout down to the grass tips : in this the upper tusks are important in pushing aside thorns and allowing the grass to be reached without endangering the eyes.

In a previous communication (Ewer, 1958) it was noted that the antero-external surface of the Warthog lower canine is highly polished, but the same is not true of the Bushpig. The significance of the polish was not at that time understood, but its origin is now apparent. It results from the brushing of the teeth against the vegetation during the continuous back-and-forth movements of the head which accompany feeding.

(iii) *Method of chewing*

Observation of the jaw action of a chewing animal is not easy. In the case of the Warthog it is difficult to make out unless the animal can be observed from directly in front : the movements of the lower tusks relative to the upper then allow the path of the lower jaw to be followed during the chewing cycle. The grinding is orthal in direction, and a complete cycle involves two " bites " of the lower jaw. The action can most easily be understood if the relative movements of the tusks of one side (say the right) are described. As the lower jaw moves upwards the upper and lower canines meet ; the mandible then moves sideways to the right, so that the lower tusk moves outwards across the upper, and the lower jaw then descends again. The jaw is then raised, without any change in its lateral displacement, until the tusks again touch, moves back sideways and inwards (to the left) and drops again to complete the cycle. The chewing is thus an orthal grinding with the lower teeth moving against the upper alternately from left to right and from right to left. This jaw action is reflected in the slantwise wear scratches which are found on both upper and lower canines where they abrade each other.

The Warthog observed at Hluhluwe were feeding almost exclusively on short green grass. As stated above, many records in the literature confirm that grass is the favourite food. The fact that when fresh grass is not available other foods may be taken is of little importance in the present context. We are concerned with determining what is the usual mode of feeding ; for it is to the predominant food that the dental and skull adaptations will be related. We will expect the skull and teeth to be adapted to grass eating, regardless of the fact that other foods are sometimes taken, and we may characterise the Warthog

as a highly selective grass plucker, the term "grazer" being a slightly misleading description.

(iv) *The use of the canines in fighting*

Since January is not the mating season, no observations of fighting between rival males could be made. One piece of behaviour which may be of some relevance to the method of fighting, was, however observed. This behaviour is referred to as "nose-play". In nose-play two animals put their snouts together with the heads held pointing downwards, so that the upper tusks are in contact; the animals then push each other until one gives way. The procedure is reminiscent of the fighting of deer with antlers interlocked. Nose-play was observed on three occasions between a young male and a full grown male and once between two full grown animals one of which was a male, and the other's sex could not be determined. The nose-play was clearly not serious fighting, but suggested fighting movements being performed in play. One would expect that in true fighting the males would take up the tusk-to-tusk position and attempt to push one another off balance. The victor would then be in a position to spring forwards and rip the other with a quick sideways and upwards cut of the sharp lower tusks. If this is correct, then the curious orientation of the enormous but rather blunt upper tusks is clearly related to a stylised method of inter-male fighting.

After reaching these conclusions, Ranger K. Tinley told me that he had seen Warthog fighting, and that the procedure was exactly as outlined above. The two animals push each other snout to snout, until finally one gives way. The victor then whips the head round and attempts to gash his rival in the side with his sharp lower canines before he can recover.

2. *The muscles*

The muscles which concern us here are the snout muscles and the muscles of mastication. The superficial muscles of the lips, ears etc., will not be considered.

The normal arrangement of the mammalian jaw muscles is such as to permit not only opening and closing of the mouth, but also some degree of movement of the lower jaw relative to the upper in both the propalinal and the orthal direction. Components in the directions indicated are normally provided by the following muscles :—

Temporalis and digastricus	backwards	propalinal
Masseter and pterygoideus	forwards	action.
Pterygoideus	mesiad	orthal action.
Masseter	laterad	

Only in cases of great specialisation of jaw movement is it therefore to be expected that there will be any major alteration in the normal arrangement of the muscles. In the Suidae no such major alteration occurs, and the differences between species concern only rather slight differences in the relative sizes and in the positions of the points of origin and insertion of the muscles. It will therefore be sufficient to describe the muscles of the Bushpig, and note the points in which those of the Warthog differ.

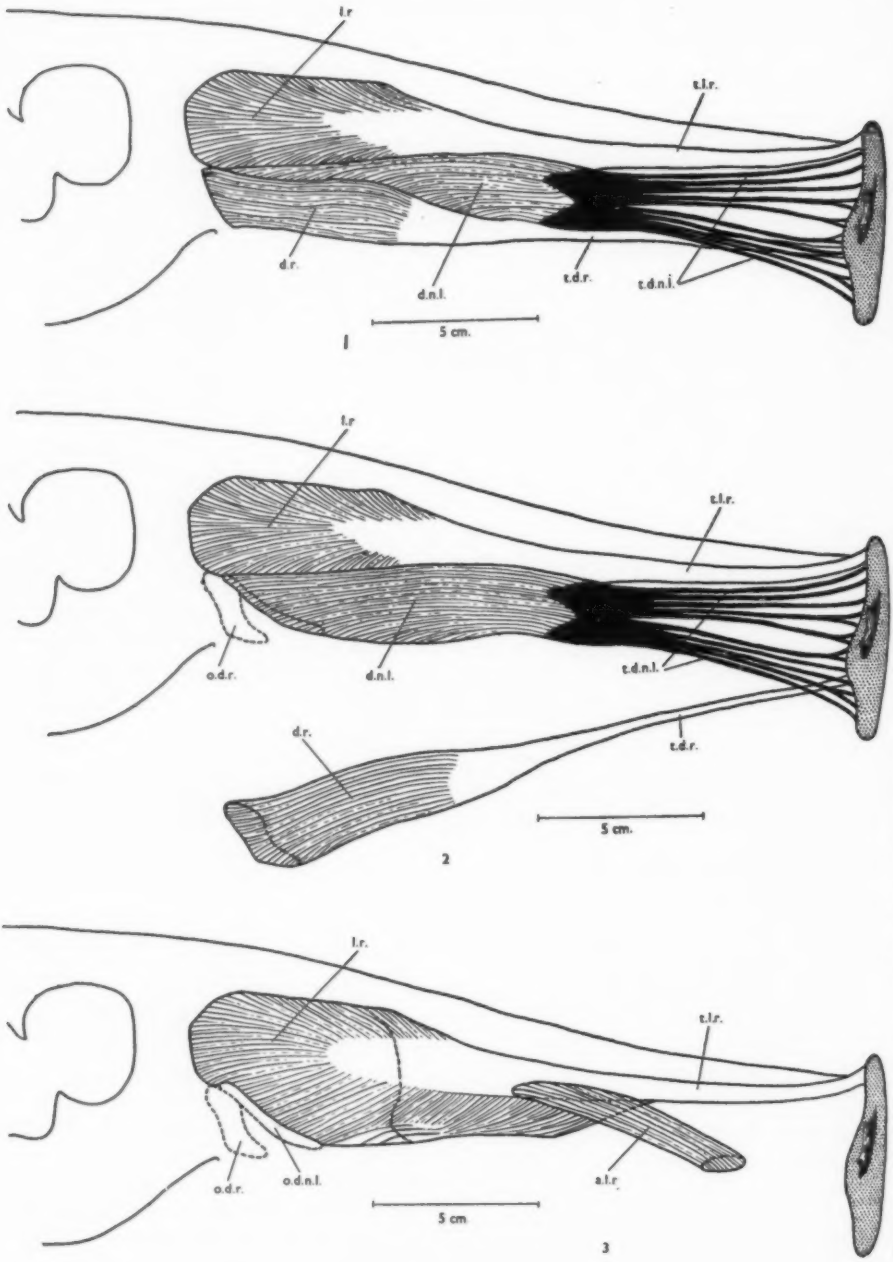


Fig. 1.—Bushpig. Dissection of snout to show muscles controlling movements of rhinarium. d.n.l., dilator naris lateralis ; d.r., depressor rostri ; l.r., levator rostri ; t.d.n.l., tendons of dilator naris lateralis ; t.d.r., tendon of depressor rostri ; t.l.r., tendon of levator rostri.

„ 2.—Bushpig. Snout muscles with depressor rostri displaced so as to expose fully the dilator naris lateralis. o.d.r., origin of depressor rostri. Other letters as in Fig. 1.

„ 3.—As Fig. 2, but with dilator naris lateralis and depressor rostri removed so as to expose fully the levator rostri and its antagonist. o.d.n.l., origin of dilator naris lateralis ; a.l.r., antagonist of levator rostri. Other letters as before.

(a) *The muscles of the snout*

The movements of the rhinarium are controlled by three muscles on either side (Figs. 1–4).

(1) Levator rostri

origin : a well marked fossa on the side of the face immediately in front of the eye, involving parts of the lachrymal, jugal and maxillary bones. The greater part of the origin is fleshy, but antero-ventrally, immediately in front of the origin of the dilator naris lateralis it becomes tendinous for a short distance (see Fig. 3). From its origin the belly of the muscle runs forward and passes into a single strong tendon running in the groove above the canine.

insertion : the distal end of the tendon splays out to insert on the skin of the rhinarium just above and mesial to the nostril (Fig. 4).

action : pulls the tip of the rhinarium up and back. From the fascia of the levator rostri tendon, a small strip of muscle runs forwards and downwards and, joining with fibres from the skin of the snout, inserts on the side of the premaxilla just above the third incisor. This slip appears to act as an antagonist to the levator rostri, as its contraction would pull the tendon of the latter forwards, stretching the muscle back to its original uncontracted length.

(ii) Dilator naris lateralis

origin : a rather narrow horizontal band, immediately below the origin of the levator rostri, extending along the horizontal ridge of bone which

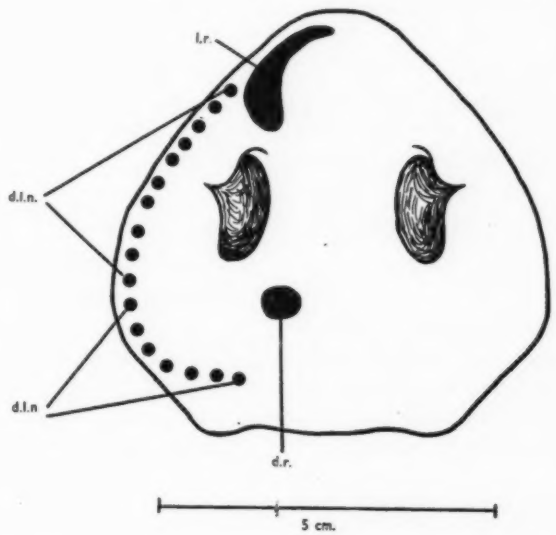


Fig. 4.—Bushpig. Rhinarium viewed from in front to show the positions of the insertions of the muscles controlling its movements. l.r., insertion of levator rostri ; d.l.n., insertions of the tendons of dilator naris lateralis ; d.r., insertion of depressor rostri.

runs out from the anterior end of the zygoma towards the infra-orbital canal (Figs. 2, 3).

insertion : the muscle runs forwards as a band of parallel fibres and, at about the level of the canines, splits up into a series of tendons. These run forwards below the tendon of the levator rostri and insert in a semi-circle all round the lateral rim of the rhinarium (Fig. 4).

action : pulls the side of the rhinarium backwards.

(iii) Depressor rostri

origin : a fossa in the maxilla immediately below the origin of the dilator naris lateralis (Figs. 2, 3).

insertion : the muscle passes anteriorly into a single strong tendon which inserts into the skin of the rhinarium at the lower internal corner of the nostril (Fig. 4).

action : pulls the rhinarium downwards and sideways.

In the Bushpig these three snout muscles are extremely large, and their origins are very clearly marked on the skull. In the Warthog the arrangement

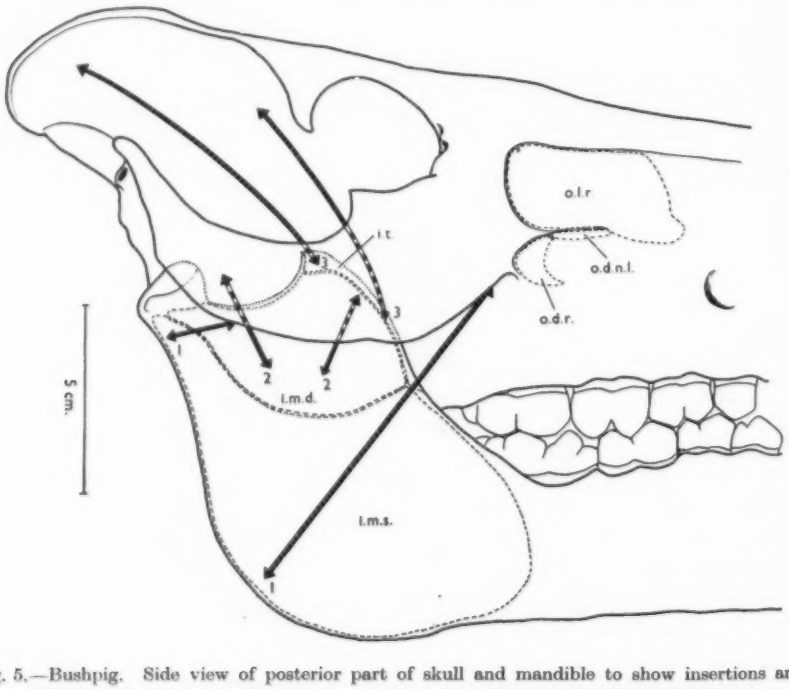


Fig. 5.—Bushpig. Side view of posterior part of skull and mandible to show insertions and lines of action of temporalis and masseter muscles. The arrows indicate the directions in which the main fibres of the muscles run. 1, 1, superficial masseter ; 2, deep masseter ; 3, 3, temporalis ; i.m.d., insertion of deep masseter ; i.m.s., insertion of superficial masseter ; i.t., insertion of temporalis ; o.d.n.l., origin of dilator naris lateralis ; o.d.r., origin of depressor rostri ; o.l.r., origin of levator rostri.

of the muscles is identical, but they are considerably smaller and their origins show less clearly on the skull.

(b) *The muscles of mastication*

(i) Masseter (Fig. 5)

α. superficial masseter.

origin : a large tendinous aponeurosis arises from the lower surface of the anterior end of the zygoma ; additional fibres originate along the lower border of the zygoma as far back as the posterior end of the jugal.

insertion : on the outer surface of the mandible covering the whole of the angle of the jaw from a point just anterior to the posterior end of M_3 to just below the condyle (Fig. 5).

action : closes the jaws, and, since the main run of the fibres is slightly sloping backwards from origin to insertion, a forward pull must be exerted on the lower jaw. In addition, since the zygoma lies lateral to the angle of the mandible, a sideways pull must also be exerted on the latter.

β. deep masseter

origin : on the inner wall of the zygoma.

insertion : on the upper part of the outer surface of the mandible, immediately above the superficial masseter (Fig. 5).

action : closes the jaws ; the fibres run some with a slight backward and some with a slight forward slope, so that little net forward or backward pull can be exerted on the mandible, but the origin lies lateral to the insertion, so a considerable sideways pull must be exerted.

(ii) Temporalis (Fig. 5)

origin : temporal fossa on the side of the head behind the orbit, clearly marked out by ridges of bone above and below.

insertion : on the tip of the coronoid process and along the anterior border of the ascending process of the mandible.

action : closes the jaws and pulls the mandible backwards.

(iii) Pterygoideus (Fig. 6).

α. pterygoideus internus.

origin : from the roughened horizontal ventral surface of the pterygoid bone immediately behind M^3, and extending along the lateral wing of the pterygoid as far as the point where the latter turns abruptly dorsally (Fig. 6).

insertion : on the inner surface of the angle of the lower jaw, from a point on the lower border anterior to the posterior end of M_3 to a point on the posterior border about 2·5 cm. below the condyle.

action : closes the jaws and pulls the mandible forwards and mesiad.

β. pterygoideus externus.

origin : over the whole of the posteriorly facing surface of the pterygoid bone, between its lateral and mesial wings.

insertion : on the inner surface of the mandible immediately below and anterior to the condyle.

action : closes the jaws and pulls the mandible forwards and mediad.

(iv) Digastricus (Fig. 6).

origin : in a strong tendinous attachment to the extreme tip of the paroccipital process.

insertion : over a wide area on the internal face of the mandible from close behind the symphysis to the level of the anterior limit of the insertion of the masseter.

action : pulls the jaw backwards, and, if not opposed by the action of the other jaw muscles, opens the mouth.

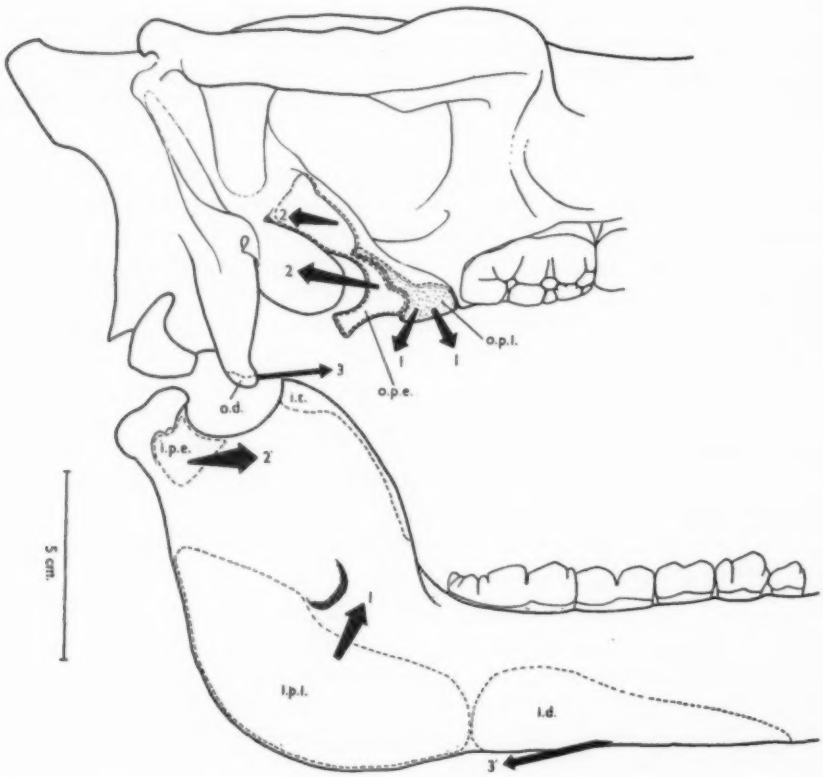


Fig. 6.—Bushpig. Above, posterior part of skull viewed from slightly below and to the right ; below, mesial surface of posterior part of left mandible. The arrows show the lines of action of the muscles. 1, 1, 1′, internal pterygoid ; 2, 2, 2′, external pterygoid ; 3, 3′, digastric ; i.d., insertion of digastric ; i.p.e., insertion of external pterygoid ; i.p.i., insertion of internal pterygoid ; i.t., insertion of temporalis ; o.d., origin of digastric ; o.p.e., origin of external pterygoid ; o.p.i., origin of internal pterygoid.

The arrangement of the muscles of mastication of the Warthog is shown in Figs. 7 and 8. The differences from the Bushpig are as follows :—

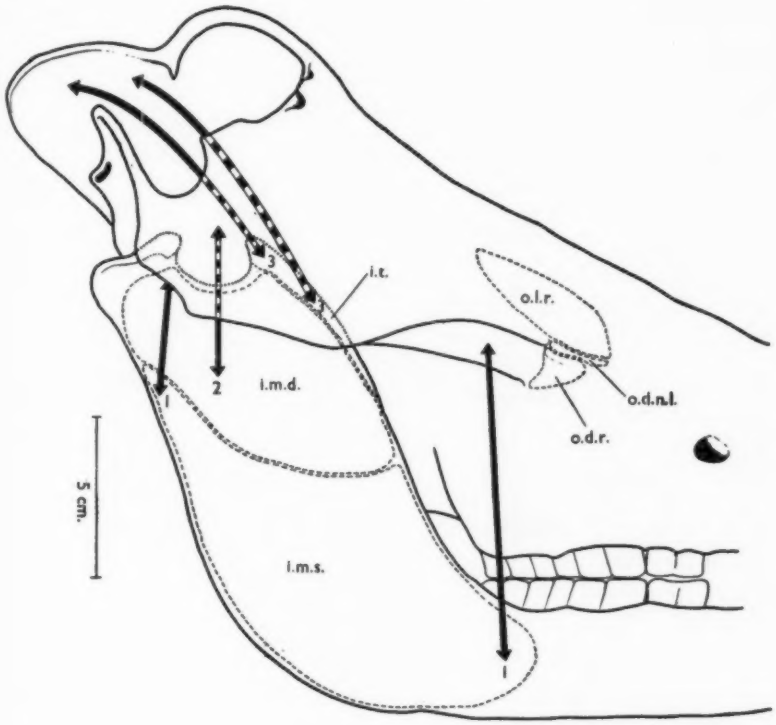


Fig. 7.—Warthog. Side view of posterior part of skull and mandible. Arrows and letters as in Fig. 5.

1. The temporalis is considerably smaller.
2. The fibres of the superficial masseter run with no backward slope from origin to insertion, so that the muscle closes the jaws and pulls the mandible laterad, but exerts no forward pull on the latter.
3. The digastricus is somewhat smaller.

3. *Offence and defence*

In this connection the canine teeth, which constitute the only weapons of the Suidae, and the protective role of the skin thickenings or warts must be considered.

In the Suidae the sharp lower tusks are the weapons most capable of inflicting wounds. In the Bushpig the upper tusks are kept short largely as a result of wear against the lower canines, and their main function would appear to be that of maintaining the sharp cutting edge of the latter. Their

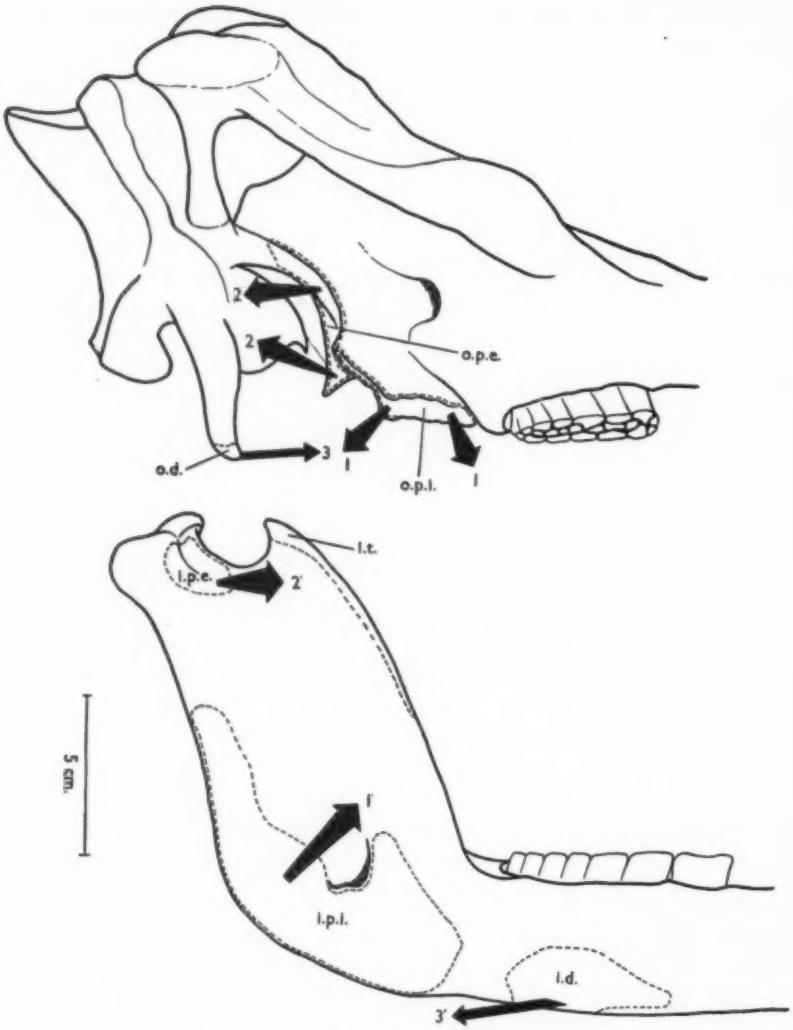


Fig. 8.—Warthog. Posterior part of skull and mandible, conventions as in Fig. 6.

role in digging, as noted previously, is probably a subordinate one. I have not been able either to watch, or to find descriptions of, fights between males in this species. Until this has been done speculation about functions of the upper tusks, apart from the obvious one of keeping the lower tusks sharp, is pointless.

In the Warthog the upper tusks are extremely large, rather blunt, and their orientation is not what would be expected if they were extensively used

as weapons. There is much individual variation, but in general the tusks of the females are much more curved in over the snout than are those of the males. Observations were made on this point at Hluhluwe, the tusk orientation being judged as belonging to one of three categories : outflaring, interme-

Fig. 9.—Anterior views of snouts of Warthog, to show differences in tusk orientation. Above, incurved ; below, outflaring.

diate or incurved (Fig. 9). Only full grown animals were scored, the previous year's young not being counted. The following scores were obtained :—

Sex	outflaring	intermediate	incurved	total scored
♂	30	2	0	32
♀	1	6	15	22

In many of the females the upper tusks were so much incurved that to deliver a blow with the point would have been quite impossible. Defence against predators is likely to be more important to the female, who guards the young, than to the male, who does not. One may therefore conclude that, as is usual in the Suidae, it is the lower tusks that are the main weapons, and that (apart from their action as sharpeners of the lower canines) the upper tusks are not important in defence. If this is so, then their incurved orientation in the female is advantageous for defence against predators, since there is a minimum

of interference with the slashing action of the lower tusks. In the male the outflaring orientation appears to be correlated with the tusk-to-tusk method of fighting, and represents a compromise between two opposing desiderata—a firm locking with the rival for tusk-to-tusk pushing demands an outwardly directed tusk, but an effective lower tusk slash sets limits to its sideways extension.

The orientation of the tusks is also to some extent correlated with the grass eating habit. More forwardly pointing tusks would probably be more effective as weapons, and are, in fact, found in many fossil genera : but for grass plucking it is essential that the tusks should not project forwards beyond the incisors. The turning of the Warthog's tusk upwards and backwards eliminates interference with the plucking of close growing grasses and the role of the tusks in pushing aside thorns without endangering the eyes has already been mentioned.

The skin thickenings and warts must now be considered. These occur in three areas :

1. Between the eye and the upper tusks.
2. Immediately below the eye.
3. Along the border of the mandible overlying the masseter muscle.

In the Bushpig there are no true warts, but the skin is thickened by dense fibrous connective tissue in these areas. That the skin thickenings are protective can hardly be doubted. The first protects the tendons of the snout muscles, the second the eye, and the third the masseter muscle. The thickenings are all placed so as to guard against attack from below. In the Warthog the skin thickenings are hypertrophied to form the large excrescences to which the animal owes both its vernacular and its scientific name. These warts are more developed in the male than in the female, which might be taken to indicate that the protection they afford is against the tusks of a rival male. Such an interpretation does not accord with the fact that scars are rarely found on the head, or with the generally held view that the Warthog in attack strikes at the side or belly. I owe to Dr Leakey the suggestion that the protection afforded by skin thickenings and warts is neither against rivals of their own species, nor predators of another, but against a more unobtrusive enemy—the thorns, spines and urticating hairs of the vegetation. The danger of a festering thorn lodged in a muscle essential for feeding is a real one both for the digging Bushpig and for the grass-seeking Warthog. Dr Leakey's previously quoted observations, on the Warthog's habit of pushing in at the bases of thorny plants to pluck grass which the less protected buck cannot reach, at once spring to mind in this connection.

Protection against thorns etc., may provide a satisfactory explanation of the primary function of suid skin thickenings, but the case of the Warthog requires further consideration. The extremely large size of the warts in the male makes it difficult to believe that their role is purely protective, and the fact that they are not nearly so large in the female demands explanation. It seems possible that in addition to their primary protective role the warts may have acquired releaser value in the male, functioning either in courtship or in threat display. Further studies on Warthog behaviour in the mating season might throw light on this point.

4. *Skull architecture*

Having considered the feeding and fighting habits, and the relevant musculature, a functional analysis of the Bushpig and Warthog skulls may now be attempted.

(a) *Bushpig* (Plate I)

The skull of the Bushpig differs from that of *Sus*, which may be considered as representing the generalised suid type, in the following particulars.

1. The snout is elongated, and much less rounded, its side walls being almost vertical and the nasals practically horizontal. The mandible and palate are constricted behind the canines, and the symphysis is elongated.

These characters clearly all relate to the digging functions of the snout. The rectangular section allows the large snout muscles to run straight from their origins to their insertions on the rhinarium, and thus to work with maximal efficiency. The elongated symphysis strengthens the snout region, and the constriction separates off the digging rhinarium from the masticatory cheek teeth. This type of separation is commonly found where functions other than eating are performed by the front of the mouth.

2. The mandible is somewhat thickened in the region of the second and third molars—a character found in more extreme form in many fossil species. The significance of this thickening is not clear : it is difficult to believe that its function is a purely mechanical one of strengthening the jaw ramus. Possibly its function may become apparent when our knowledge of the skulls of fossil forms and the behaviour of extant species is more extensive.

3. In the male the flange of bone lying over the alveolus of the upper canine is much enlarged. It forms a flat plate of bone extending up outside the tendons of the snout muscles almost to the level of the top of the muzzle. The tips of the maxillary flanges and the edges of the snout beside them are expanded into thick rugosities, and the overlying skin is dense and hard. Since there is no such development in the female the enlarged bony flanges are presumably connected with fighting rather than digging. It seems possible that they may be important in snout-to-snout pushing, for they are so placed as to provide a satisfactory *point d'appui*, which may be necessary in the absence of large spreading tusks.

The skull of the Bushpig thus differs from that of a generalised suid in certain features which are associated with the digging functions of the snout. The significance of other differences, the mandibular thickening and the maxillary flange, remains obscure. These may possibly be related to fighting techniques, but until observations on this subject have been made no certainty can be reached.

(b) *Warthog* (Plate 2)

The Warthog skull is of extremely peculiar construction, differing widely from that of *Sus* both in the snout and in the posterior region. The characters of the snout are explicable in terms of the large upper canines and the reduced importance of digging with the rhinarium. In the Bushpig the dominating importance of rhinarium digging is reflected in the elongated and vertical sided

snout : in the Warthog the dominance of the upper canines is reflected in exactly the reverse characters ; the snout is relatively short, and the nasals are rounded, so as to give maximum strength and rigidity without undue increase in weight, the weight carried by the snout in the large upper tusks being already considerable.

The posterior part of the skull is characterised by the unusual position of the eyes, high up and far back on the head, the very long paroccipital processes and the extreme reduction of the postorbital region. The latter characteristic is a reflection of the diminished importance of the temporalis muscle. This is comprehensible in terms of the animal's eating habits : the quick snapping jaw action for which the temporalis is responsible is no longer necessary in grass plucking, and it is the masseter and pterygoideus muscles which are now the most important in mastication. The raising of the whole posterior region of the skull is less simply explained. The small difference in the angle of insertion of the masseter muscles from those of the Bushpig has already been mentioned, and this reflects the fact that orthal movement of the lower jaw has increased in importance : but this change could easily be made with much less drastic modification of skull shape than is actually found, so the explanation must be sought in other terms.

Colbert (1945), in dealing with the adaptations of the carnivorous and herbivorous dinosaurs, has pointed out that for the scissor like action of the teeth required for meat slicing the jaw articulation must lie on the same level as the tooth row : this is the condition in the carnivorous Saurischia. When a crushing action is required, a more nearly parallel approach of the lower jaw to the upper results if the articulation lies in a different horizontal plane from the tooth row, a principle exploited in the type of pliers known as the vice-grip. In the herbivorous Ornithischia this is achieved by a glenoid lying well below the level of the tooth row. In herbivorous Mammalia the same result is produced by a glenoid lying well above the level of the tooth row. The peculiarities of the posterior part of the skull of the Warthog are explicable in these terms. The glenoid lies high above the alveolar margin, very much higher than in the Bushpig, and, of course, the height of the condyle on the mandible shows a corresponding increase (see Table 1). This arrangement allows the grinding third molars to come together along the greater part of their length, and it is the raised glenoid, rather than any question of angles of muscular insertion, which determines the peculiar raising of the back of the Warthog skull. This, in turn, necessitates a lengthening of the paroccipital process if the digastricus is to remain in a position permitting it to act as a jaw opener, and it also inevitably raises the position of the orbits.

The orbits are, however, not only raised, but carried backwards by an elongation of the lachrymals. This is to be explained partly in terms of the greater protection to the eye thus afforded, rather than in terms of jaw mechanics. The position of the eye is also correlated with the animal's feeding habits. Warthog feed largely by day and in the open, so that watching for the approach of an enemy may be important. In feeding the head is pointed downwards, and in this position carrying of the eye morphologically

backwards is equivalent to raising it higher above the ground, into a position more advantageous for seeing an approaching enemy.

Three distinct selective forces have thus been at work in influencing the shape of the posterior portion of the Warthog skull : the diminished importance of the temporalis has led to a reduction of the postorbital length ; the increased importance of grinding with the back teeth has led to the raising of the glenoid, and the need for protection of the eyes and for keeping a good look out during feeding has led to the elongation of the lachrymal and posterior movement of the orbits.

TABLE 1

The first column gives the height of the glenoid above the level of the grinding surface of M^3. The third column gives the glenoid height as a percentage of the basilar length.

Species		Glenoid ht. (mm.)	Basilar length (mm.)	Relative glenoid ht.
Potamochoerus	♀	60	296	20·3
	♀	50	300	16·7
	♀	43	321	13·8
	♂	52	303	17·2
	♂	55	311	17·7
	?	52	—	—
Phacochoerus	♀	100	306	32·7
	♂	78	293	25·6
	♂	80	290	26·6
	♂	91	—	—
	♂	98	305	32·1
	♂	99	314	31·5
Hylochoerus	?	60	344	17·4

III. THE SKULL OF THE FOREST HOG, *Hylochoerus*. (Plate 3)

I have not had the opportunity to study the behaviour of the Forest Hog, *Hylochoerus meinertzhageni* Thomas, nor to dissect its muscles, but a few points of interest emerge from a consideration of its skull.

Hylochoerus is very different in its feeding habits from either of the other living species. It is a specialised vegetarian, and its principal food is the soft tips of dicotyledonous plants (Woodhouse, 1911, Zukowsky, 1921, Copley, 1949, Stockley, 1950, 1952). Long grass is, according to Stockley (1950) sometimes eaten while it is still young and relatively soft. There is no satisfactory record of this species ever digging up food with its snout. It may thus be characterised as a specialised browser.

In correlation with the purely vegetarian diet, the premolars are reduced, as in the Warthog, but the concentration on soft food has not necessitated any great specialisation of the molars. The third molars are brachydont, not much elongated, and all three molars are used simultaneously. The wear scratches made by upper and lower canines against each other are almost vertical, indicating a chopping rather than a grinding jaw action. The incisors

are reduced to $\frac{1}{2}$, and are rather like those of the Warthog, while the lower canines show a Warthog-like polish on the antero-external surface. These facts would seem to indicate that, like the Warthog, *Hylochoerus* is a nice and discriminating feeder. Observations on precisely how this animal takes its food are much to be desired.

The upper tusks are not quite so large as those of the Warthog and are less upturned. Apart from this they are rather similar and wear against the lower teeth in the same sort of way.

The pre-nasal bone is usually firmly fused to the nasals and premaxillae and supports a very large rhinarium, of a type quite unsuited to digging.

It has frequently been said that in its skull architecture *Hylochoerus* is intermediate between *Potamochoerus* and *Phacochoerus* (see, for instance, Bouet & Neuville, 1930). This statement is based on a fundamental misunderstanding of the whole question ; on a geometrical, rather than a functional approach. Since the incisors (apparently) perform a similar function in food selection, and since the tusks are similar, we would expect that in the incisor region and in all those features associated with the carriage of the tusks and with defence against the tusks of rivals, the skull of *Hylochoerus* should resemble that of *Phacocoeurs*. On the other hand, since the jaw action is chopping, not grinding, we would expect to find that in all the features of the skull which reflect the jaw action the resemblance to *Potamochoerus* would be close. Associated with the loss of the digging functions of the snout we may expect to find features not shown by either of the other genera, although the resemblance to *Phacocoerus* should be the closer. The skull of *Hylochoerus* is, in fact, not to be regarded as an intermediate, but rather as embodying a number of adaptive features, some of which are shared with the Warthog and others with the Bushpig.

These expectations are in fact fulfilled. The rounded nasals and the whole conformation of the incisor region in both upper and lower jaws are very similar to the condition in *Phacochoerus*. The grinding adaptations of the posterior part of the skull are absent : the glenoid is not raised (see Table 1), the paroccipital processes are relatively short, and the conformation of the posterior part of the skull and mandible is potamochoeroid. The eyes are, by their position, less protected than those of *Phacochoerus*, and it may be in compensation for this that the sub-orbital wart is enormously hypertrophied. The bone of the zygoma underlying the wart is roughened and thickened and provides a firm anchorage for it. The wart protecting the tendons of the snout muscles is absent. This may reflect the diminished importance of the muscles, but may also be related to the protection afforded by the almost horizontal backwardly curved canines, which may make a wart unnecessary.

One characteristic of the *Hylochoerus* skull remains unexplained. The occiput bears a vertical ridge of bone, and is extremely wide. This increase in width would, other things being equal, lead to an increase in the size of the braincase. Unless the brain is correspondingly enlarged some compensating reduction in the volume of the braincase is to be expected. Since no muscles are attached to the skull between the temporal crests, there is no need to preserve the normal external contour in this area, and the necessary compen-

sation is achieved by a lowering of the skull roof ; with the result that it has a highly characteristic collapsed appearance, like a badly baked cake. The characters of the occiput indicate that the neck muscles are more developed than in either of the other two living genera, but the reason for this is not clear. The tusks are not as big as those of the Warthog, so that the large neck muscles cannot be necessary merely because of the weight of the tusks. Possibly they are associated with a fighting technique which is different from that of the Warthog, but I have not been able to discover any account of *Hylochoerus* fights. Thus, before the adaptations of the *Hylochoerus* skull can be fully understood, detailed observations both on the technique of fighting between males and on the prehension of the food are required.

IV. FOSSIL SPECIES

A study of the Bushpig and the Warthog has shown which features in skull architecture are associated with specialisations for digging with the snout, for a grinding action of the molars, and for protection against thorns, etc. Although fossil material consists mainly of teeth, isolated or associated only with small fragments of the jaws, there are some specimens sufficiently complete to be worth consideration in these terms. I have not been able to examine all the relevant material, and the remarks which follow are therefore very incomplete.

Of the specimens available to me, the most interesting are those of *Phacochoerus antiquus* Broom. The type, an immature skull, was described by Broom (1948), and additional material by Ewer (1956). The cheek teeth differ from those of the living Warthog in minor details, but the skull shows much greater divergence. The snout is less rounded, indicating that Broom may have been right in suggesting that the upper canines were small compared with those of the modern species. The jugal is much less elongated, and the glenoid lies at a lower level than in the modern species. The adaptations of the posterior part of the skull for a grinding action of the cheek teeth are therefore still very incomplete.

A number of authors have pointed out that alterations in habit would be expected to preceed, rather than to follow, changes in structure (Lorenz, 1950, Ewer, 1952, Haldane & Spurway, 1954). Obviously, if an animal does not eat grass, then there can be no selective pressure to improve its adaptations to this habit, no accumulation of mutations leading to increased grinding specialisations. One would therefore suppose that, although its skull adaptations are incomplete, *Phacochoerus antiquus* must have been a selective grass-eater, like its modern descendant. This can be shown to be the case, for although the lower canine is rather badly preserved, sufficient of the enamel remains in one specimen to show that the typical Warthog polish was present on the antero-external face. We may therefore infer that its method of feeding was like that of the living form.

The type mandible of *Potamochoeroides shawi* (Dale) was described by Dale (1948), and additional material by Ewer (1958). This is a species showing some increase in length and hypsodonty of the third molars, but is otherwise reminiscent of *Potamochoerus*. The snout, however, shows none of the digging

specialisations characteristic of the latter genus, and we can say with confidence that digging was not of great importance in the life of this species. One immature specimen preserves the glenoid. It does not appear to lie at a higher level than in a Bushpig of comparable size, and the general facies of the posterior region of the skull is potamochoeroid. In addition, the wear scratches on the upper tusks are approximately vertical. From these facts it follows that the jaw action was still chopping rather than grinding. At the same time the changes in the third molars can only be interpreted as adaptations to a concentration on hard vegetable food and abandonment of the omniverous habit. Hence it appears that in this lineage the first vegetarian specialisation to evolve was modification of the third molars : only at a later stage, of which fossil evidence is not yet available, was a grinding jaw action adopted.

This is, of course, the sequence to be expected on theoretical grounds. A change in feeding habits so that grass becomes a more important component of the dietary, for whatever reason it occurred, would immediately confer selective advantage on any mutations tending to increase the grinding efficiency of the cheek teeth. As a result there would be accumulation of mutations converting the short low-crowned bunodont cheek teeth into elongated high-crowned multi-cusped grinders. Once this process is well under way—but not before—there will be selective advantage in a more effective grinding action of the jaws as the food is masticated. Here, again, habit must change before structure—until the animals attempt to grind their food as best they can with the skulls and muscles they have got there can be no accumulation of mutations causing changes in skull architecture which give greater grinding efficiency. There will therefore be selection first for the habit of moving the jaws sideways during chewing and, once this is established, for corresponding adaptations in skull structure. The fossil record would therefore be expected to show precisely what it does—to wit that the teeth are " ahead " of the skull in the process of evolutionary change from omnivore to specialised grass eater.

V. SUMMARY

The relevance of a functional understanding of the skull architecture of living forms to the study of fossils is pointed out.

A brief description of the food and feeding habits of the extant Bushpig (*Potamochoerus koiroptamus*) and Warthog (*Phacochoerus africanus*) is given, and the muscles of mastication and those controlling the movements of the rhinarium are described. The features in the skull of the Bushpig which are related to the digging habit and those of the Warthog which are related to its grass eating habit are pointed out.

The adaptive features in the skull of the Forest Hog (*Hylochoerus meinertzhageni*) are discussed.

The way in which an analysis in terms of the functional basis of skull characteristics may throw light on the modes of life of fossil suids is briefly indicated.

VI. ACKNOWLEDGMENTS

My thanks are due to the South African Council for Scientific and Industrial Research for a Research Grant, during the tenure of which this work was

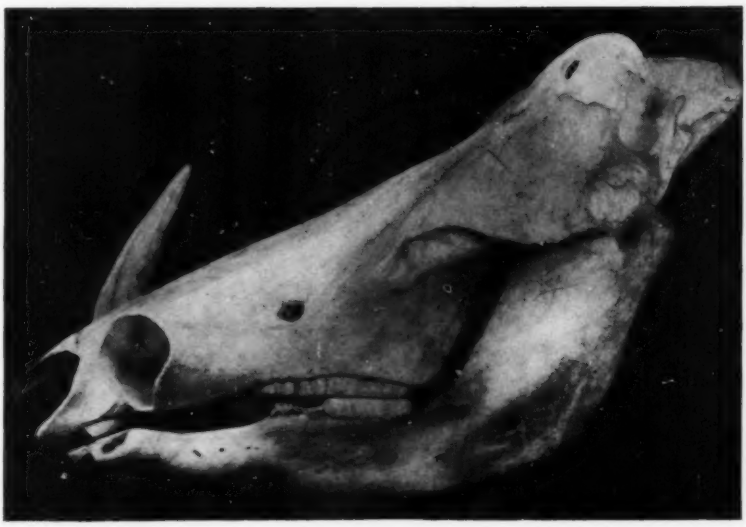
PROC. ZOOL. SOC. LOND. VOL. 131. EWER. PL. 1.

a

b

Skull of Bushpig: lateral and latero-ventral views.

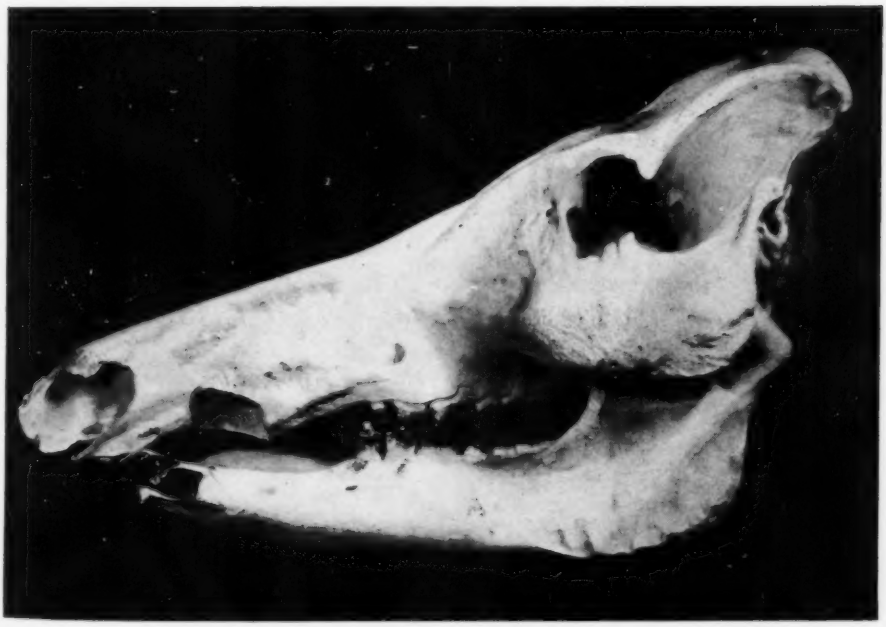
a



b

Skull of Warthog: lateral and latero-ventral views.

a



b

Skull of Forest Hog: lateral and latero-ventral views.

carried out. I am indebted to the Natal Parks Board for affording me special facilities to work in the Hluhluwe Reserve. I should like particularly to thank Chief Conservator P. Potter and Scientific Officer C. Ward for the assistance they gave me during my stay at Hluhluwe. I am also grateful to Dr M. Webb and Mr J. Skead for getting me Bushpig heads for dissection, to C. K. Brain for taking the photographs of Bushpig and Warthog skulls and to Dr L. S. B. Leakey for many useful suggestions and helpful discussions together with the gift of a *Hylochoerus* skull.

VII. REFERENCES

BOUET, G. & NEVILLE, H. (1930). Recherches sur le genre *Hylochoerus*. *Arch. Mus. nat. Hist. nat. Paris*, **5**, 215–304.

BROOM, R. (1948). Some South African Pliocene and Pleistocene mammals. *Ann. Transv. Mus.* **21**, 1–38.

COLBERT, E. H. (1945). The dinosaur book. New York : Amer. Mus. nat. Hist.

COOKE, H. B. S. (1949). The fossil Suina of South Africa. *Trans. Roy. Soc. S. Afr.* **32**, 1–44.

COPLEY, H. (1949). The pigs of Kenya. *Nature in E. Afr.* **2**, 6–10.

DALE, M. M. (1948). New fossil Suidae from the Limeworks Quarry, Makapansgat, Potgietersrust. *S. Afr. Sci.* **2**, 114–116.

EWER, R. F. (1952). A note on adaptation. *New Biol.* **13**, 117–119.

EWER, R. F. (1956). The fossil suids of the Transvaal Caves. *Proc. zool. Soc. Lond.* **127**, 527–544.

EWER, R. F. (1958). The fossil Suidae of Makapansgat. *Proc. zool. Soc. Lond.* **130**, 329–372.

FITZSIMONS, F. W. (1920). *The natural history of South Africa*. London : Longmans Green & Co.

GUIRAUD, M. (1948). Contribution a l'étude du *Phacochoerus aethiopicus* (Pallas). *Mammalia, Paris* **12**, 54–66.

HALDANE, J. B. S. & SPURWAY, H. (1954). A statistical analysis of communication in *Apis mellifera* and a comparison with communication in other animals. *Insectes sociaux* **1**, 247–283.

KIRBY, F. V. (1896). *In haunts of wild game*. Edinburgh & London : Blackwood & Sons.

KIRBY, F. V. (1899). *Sport in East Central Africa*. London : Rowland Ward Ltd.

LEAKEY, L. S. B. (1958). Some East African Pleistocene Suidae. *Fossil mammals of Africa*. No. 14. London : Brit. Mus. (nat. Hist.).

LORENZ, K. (1950). The comparative method in studying innate behaviour patterns. *Symp. Soc. exp. Biol.* No. **4**, 221–268.

PHILLIPS, J. F. V. (1926). " Wild pig " (*Potamochoerus choiropotamus*) at the Knysna : notes by a naturalist. *S. Afr. J. Sci.* **23**, 655–660.

ROOSEVELT, T. (1910). *African game trails*. New York : Scribners.

ROOSEVELT, T. & HELLER, E. (1914). *Life histories of African game animals*. London : John Murray.

SHORTRIDGE, G. C. (1934). *The mammals of South West Africa*. London : Heinemann.

STEVENSON-HAMILTON, J. (1947). *Wild life in South Africa*. London : Cassell.

STOCKLEY, C. H. (1950). Mammal notes. *Nature in E. Afr.* **3** (2), 3–4.

STOCKLEY, C. H. (1952). Giant forest hog. *Country Life, Lond.* **112**, 341–342.

WATSON, J. M. (1949). The wild mammals of Teso and Karamoja II. *Uganda J., Lond.* **13**, 39–60.

WOODHOUSE, C. W. (1911). Some East African pigs. *J. E. Afr. Uganda nat. Hist. Soc.* **2** (3), 40–46.

ZUKOWSKY, L. (1921). Mitteilungen über eine anscheinend neue Form von *Hylochoerus* aus dem Winterhochland, vom Mutjekgebirge und vom Meru-Berge. *Arch. Naturgesch.* Abt. A. **87** Heft 1, 179–191.

NOTICE

["Proceedings", Vol. 130, Part 4, was published on the 20th June, 1958.]

Printed by Taylor & Francis, Ltd., Red Lion Court, Fleet Street, London, E.C.4.

INSTRUCTIONS TO AUTHORS.

Two volumes of the Society's " Proceedings " each of four parts, are issued annually, and the " Transactions " at irregular intervals. Papers for publication should be addressed to: The Editor, Zoological Society of London, Regent's Park, London, N.W.1. Papers forwarded for publication are understood to be original works and to be offered to the Zoological Society alone unless the contrary is stated. The copyright becomes the property of the Society when papers are accepted. The Scientific Committee draws the attention of authors submitting papers for publication by the Society to the following regulations. If the conditions are not observed, papers will be returned.

MSS. submitted for publication must be type-written with double spacing between the lines and good margins, and must be in final form for printing. They must be typed on one side only of each sheet, and the sheets must be numbered. Papers must include a **Table of Contents** and a **Summary** containing a succinct account of the subject, results obtained and conclusions. The summary must not exceed one-twentyfifth of the text in length. The positions for text-figures and tables must be indicated in pencil in the margin. The metric system should be used for all measurements. Footnotes are to be avoided.

References in the text must be cited by giving the author and date, e.g. " Smith (1957) stated . . . " and the complete references arranged in alphabetical order of the authors' names at the **end of the paper.** They must contain the following information, in the order given: (1) The author's name(s) and initials(s). If there is more than one author the ampersand (&) not the word " and " must be used between the last and the penultimate names. (2) The publication date of the paper, in brackets. If reference is made to more than one paper by the same author(s) published in a single year, the suffixes a, b, etc. should be used, e.g. (1951 a). (3) The full title of the paper. Only the first word, except proper names, may have a capital letter. Titles in German have capitals as in the original journal. (4) The title of the journal abbreviated according to the " World list of scientific periodicals ". (5) The volume number in arabic numerals without the prefix " vol." and the number of the first page in arabic numerals, without the prefix " p.". If the journal has appeared in more than one series the series number must appear in brackets before the volume number, e.g. (3), (n.s.), (B).

Where the reference is a separate book the title must be underlined and the place of publication given.

References thus appear as follows:—

PARRINGTON, F. R. (1956). The patterns of dermal bones in primitive vertebrates. *Proc. zool. Soc. Lond.* **127**, 389.

COWLES, R. B. (1956). Sidewinding locomotion in snakes. *Copeia* **1950**, 211.

ROMER, A. S. (1956). *Osteology of the reptiles.* Chicago.

GREEN, J. (1956). Variation in the haemoglobin content of *Daphnia*. *Proc. roy. Soc.* (B) **145**, 214.

Illustrations, particularly plates, are expensive and should be kept to the minimum. It is important that a scale, in either centimetres, millimetres or microns should appear on all drawings and photographs. The size of the original must *not* be shown by a multiplying factor, e.g. ×120 or ×1/10 because such factors may be altered in the process of block-making.

COPYRIGHT.—Any communication made to the Society will, if accepted for publication, become the property of the Society, and will not be returned to the author, except for the purpose of comparison with the proof when set up in type. The author assigns to the Society the copyright of the text and illustrations in consideration of their paying the cost of production and granting twenty-five separate copies free of charge. The Scientific Committee is always ready to give authors who apply for it permission to reproduce matter that they have contributed to the Society's " Proceedings " and " Transactions ".

A leaflet giving fuller details of the Society's instructions to authors may be obtained gratis on application to the Librarian and Clerk of Publications.

LIST OF CONTENTS

Vol. 131

Part 1 (pp. 1-155)

Page

Bishop, M. W. H. and Crisp, D. J.
The distribution of the barnacle *Elminius modestus* Darwin in France. (2 figures) 109

Cain, A. J. and Harrison, G. A.
An analysis of the taxonomist's judgment of affinity. (1 figure).. 85

Crisp, D. J. See Bishop, M. W. H.

Duncan, C. J.
The anatomy and physiology of the reproductive system of the freshwater snail *Physa fontinalis* (L.) (13 figures)..... 55

Ewer, R. F.
Adaptive features in the skulls of African Suidae. (3 plates and 9 figures) 135

Green, J.
Dactylopusioides macrolabris (Claus) (Copepoda : Hacpacticoida) and its frond mining nauplius. (13 figures)..... 49

Harrison, G. A. See Cain, A. J.

Hewson, Raymond
Moults and winter whitening in the mountain hare *Lepus timidus scoticus*, Hilzheimer 99

Hinde, R. A.
The next-building behaviour of domesticated canaries. (10 figures) 1

NOTICE.

" Proceedings ", Vol. 130, Part 4, was published on 20th June 1958.